

USEFULNESS OF CERTAIN DIALLEL ANALYSES
UNDER NORMAL AND DEVIATING CONDITIONS

A model experiment
using diallel crosses
between erectoid mutants
of the barley variety Bonus

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Lund 1975

Acknowledgments

I am deeply grateful to Professor Erik Åkerberg, former director of the Swedish Seed Association, Svalöf, for his guidance, encouragement and generously providing me all possible facilities for this study. Without his support and inspiration, it would have been hardly possible to finish this study. Also I acknowledge with gratitude my indebtedness to those authorities and organizations who so generously granted me economic support.

My special gratitude and thanks are due to Docent Göran Persson of the Swedish Seed Association, Svalöf, for his constructive guidance and suggestions throughout this investigation. I greatly appreciate his personal concern and the practical assistance I received during the various phases of this work.

I wish to thank also Professor Åke Gustafsson, former head of the Institute of Genetics, Lund for his interest and inspirational aid and for facilities which have been extended to me.

I am greatly indebted to Professor Arne Lundqvist and Docent Gunnar Ising, Institute of Genetics, Lund, for their guidance and great interest in this work. Their active help and fruitful criticism paved the way for the work.

Without mentioning special names, I should like to thank all members of the Swedish Seed Association, Svalöf, and all others who contributed to this study.

My thanks also go to Mrs. Madeleine Gustafsson, Miss Anne Berg and Miss Ann-Marie Åkesson for typing the manuscript.

I should like to convey my thanks to Bangladesh Agricultural University, Mymensingh, Bangladesh, for granting me a financed study leave (IDA-scholarship) for this work.

Finally, I wish to thank all other institutions and individuals who have in any way contributed to the completion of the present work.

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Introduction

The theory of diallel crosses in genetic analysis of populations has received considerable attention in recent years. The diallel cross techniques have become widely used experimentally, especially by plant breeders, to whom its chief value is that it enables a number of potentially useful breeding lines to be evaluated simultaneously and as early as in the F_1 generation. The method has proved to be of considerable value to plant breeders in determining the type of breeding system to use and selecting breeding materials that show the greatest promise for success. It has been used successfully by quantitative geneticists attempting to gain a better understanding of the nature of gene action involved in determining quantitative traits, which are of the utmost importance in agriculture as well as in evolution. Methods that permit identification of outstanding offspring in early generations of the hybrids would clearly be advantageous, but such methods are not numerous, nor without controversy and limitations.

Much has been written on the theory and analysis of the diallel cross by Hayman (1954a, b; 1957; 1958a, b; 1960a, b), Griffing (1956), Kempthorne (1956), Aastveit (1961), Johnson and Aksel (1959) and others, and the plant breeders who have utilized the diallel cross technique are too numerous to mention. Several diallel cross techniques have been proposed and applied to diverse problems. Thus, Griffing (1950, 1956a, 1956b), and Matzinger, Sprague, and Cockerham (1959) have considered the utility of diallel crosses in investigations of the notions of general and specific combining ability in plant and animal materials. Another application to a practical problem - the early generation selection of parental materials in breeding programs - has been discussed by Jinks (1955), Allard (1956b, 1956c), and Whitehouse, Thompson, and Valle Ribeiro (1958). The application to still another problem - the investigation of genotypic-environmental interactions - has been considered by Matzinger and Kempthorne (1956), Allard (1956a), Matzinger, Sprague, and Cockerham (1959). The theory of diallel crosses, and procedures for estimating certain genetic parameters in terms of gene models in varying

degrees of complexity, have been discussed by Griffing (1950, 1956a, 1956b), Hayman (1954a, 1954b, 1957, 1958, 1960a, 1960b), Jinks (1954, 1956), Dickinson and Jinks (1956) and Kempthorne (1956).

Diallels have been used primarily to estimate genetic variances when parents are either random individuals or inbred lines from a random-mating population and to estimate general and specific combining ability effects from crosses of fixed lines. The purpose of making a diallel cross is to obtain knowledge of the kinds and magnitudes of variability which contribute to differences among the lines. Yates (1947) has presented a diallel analysis. This has been modified and stated in terms of biometrical genetic parameters by Jinks and Hayman (1953) and further by Hayman (1954a, b) and Jinks (1954). Kempthorne (1956) has discussed these methods of analysis in terms of variances of inbred parents, crossbred offspring and the covariance between parents and offspring. Griffing (1956) has classified the four different ways in which at least a $p(p - 1)/2$ set of crosses can be obtained, and has discussed the analysis of each in terms of the variances of general and specific combining ability. Also concerned with maternal effects, Jinks (1954) and Jinks and Broadhurst (1963) have used still another analysis of a diallel cross.

In spite of so many and seemingly different analyses presented in the literature, one that has been widely accepted and extremely used for its usefulness to practical breeding, is that presented by Jinks & Hayman (1953) and Hayman (1954a, b). A diallel crossing system can be defined as one in which p genotypes are chosen and intercrossed. The parental genotypes are usually inbred lines, but they can also be individuals, clones, etc. A full diallel cross consists of p^2 possible matings among a set of p parental lines including $\frac{1}{2} p(p - 1)$ pairs of reciprocal crosses. These p^2 combinations are conveniently divided into three groups: (1) the p parental combinations; (2) one set of $\frac{1}{2} p(p - 1)$ F_1 combinations and (3) the set of $\frac{1}{2} p(p - 1)$ reciprocal F_1 combinations. Diallel crossing techniques vary with inclusion or absence of parental inbreds and/or reciprocal F_1 s, and with sampling assumptions. There are two alternative sampling assumptions: (1) Parental genotypes are assumed to be a random sample from some population about which inferences are to be made, and (2) the parental genotypes are deliberately chosen and can not be regarded as a random sample from

any population e.g. the experimental material constitutes the entire populations about which inferences are to be made.

The analysis proposed by Jinks and Hayman (1953) includes parents and one or both sets of F_1 crosses, i.e. in method (1) parents, one set of F_1 s, and reciprocal F_1 s are included (p^2 combinations); and method (2) parents and one set of F_1 s are included, $\frac{1}{2} p(p + 1)$ combinations. The methods of Hayman obtain sufficient information from the grouping of crosses from a diallel set into arrays rather than by using many families from one cross. In this context an array is defined as one variety and all the crosses involving it. This analysis gives, among other things, information about the average additive effects of the genes, about the effects of the heterozygosity, about the dominance of the genes in each parent, and about gene interaction. High manifestation of a character in a cross can thus be attributed either to heterozygosity (unfixable on inbreeding) to additivity of gene action or to non-additivity of gene action, i.e. to interaction if the non-additivity is between loci or to dominance relationship if the non-additivity is within loci. It can also be decided, in those cases where dominance relationships are effective, whether the high manifestation is due to dominant genes, to recessive genes or to a balanced grouping of dominants and recessives. Furthermore, the analysis should demonstrate whether any of the varieties used as parent contains the complement of dominant or recessive genes available in the parent used. If the high manifestation of a character is due to the possession of either dominant or recessive genes it becomes possible to assess the chances of obtaining selections which will transgress the parent which contains most dominant or recessive genes. The theory and analysis of diallel crosses as presented by Jinks and Hayman (1953) and Jinks (1954), and extended by Hayman (1954a and b) has one of its features the V_r, W_r distribution which is used to investigate simultaneously the genetic properties of a group of homozygous parents. Dominant relationships can be graphically represented in terms of V_r , the variance of all the offspring of the r th parent, and W_r , the covariance between these offsprings and their non-recurring parents. The position of (V_r, W_r) on the graph reveals the relative proportions of dominant and recessive genes in r th parent. This method thus seems to offer promise in the study of quantitative characters - an early identification of parents whose hybrids are most likely to respond to selection.

This method of diallel analysis is primarily based on the following

assumptions:

- (1) homozygous parents
- (2) diploid segregation
- (3) no reciprocal difference
- (4) no epistasis (no non-allelic gene interaction)
- (5) no multiple alleles
- (6) uncorrelated gene distribution and no linkage
- (7) no genotype-environmental interaction within locations and years (except within certain prescribed limits).

A reliable assessment of the relative values of the lines under list therefore, depends to a large extent upon the fulfilment of these conditions. The first five of these assumptions are general to all biometrical analyses. The resultant effect on the diallel analysis due to the failure of any of the last two conditions is not known till at present. The only reported evidence comes from Hill (1964) who only simulated the effect of correlated gene distribution in a diallel cross. The chief difficulty in estimating the results due to failure of either of these conditions is presented by lack of suitable material that is ideally and unambiguously suited for such investigations. Also, the amount of experimental work which has so far been carried out to determine precisely what happens in the event of a failure of one or more of these other conditions is so limited and inconclusive as to preclude any inferences to be made. The results from a particular diallel cross can be interpreted in a comparatively clear manner if these conditions are fulfilled but difficulties inevitably arise in interpretation when assumptions are not satisfied. Unfortunately, it is at this point that our knowledge of diallel cross is at its weakest.

The most extensive work on this problem is that of Jinks (1954, 1955), who was interested primarily in the effects of non-allelic interactions on the array covariance-variance graph. He found the regression line of W_r on V_r , which normally expected to have a slope of 1, to depart significantly from its expectation when gene interactions were presented. Though non-allelic interactions are the most common source, they are by no means the sole cause of disturbance in the W_r/V_r graph. Non-random gene distribution can also produce characteristic upsets on the graph (Hill, 1964), but in practice the main difficulty has been to obtain data which will display their effects in such a way as to enable them to be clearly separated from those of non-allelic interactions.

The Jinks-Hayman method has, however, come under criticism mainly from Kempthorne (1956) and Gilbert (1958). Since the parents of interest to breeders of self-pollinated crops will almost always be a selected sample, the appropriate sampling assumption is that the experimental material itself constitutes the entire population about which inferences are to be made. Kempthorne's basis of criticism is that "the diallel cross must be interpreted in terms of some population which has given rise to the homozygous parents in inbreeding. If such a population does not exist then the whole analysis ... is likely to lead nowhere. From quite another viewpoint one may question the value of estimating additive variance and so on ... unless the estimated quantities are measures of the characteristics of a definite population." Since the parents of primary interest to breeders of self-pollinated crops will usually not have been derived by inbreeding from some definite population, Kempthorne evidently considers that the Jinks-Hayman type of analysis of diallel crosses has little practical value as an aid in the improvement of self-pollinated crops. Hayman (1957, 1958a, 1960a) has considered this criticism and has discussed some additional aspects of the theory and analysis of diallel crosses. Gilbert (1958) has also criticized the assumptions on which the Jink-Hayman analysis is based, concluding that the method is not directly relevant to plant breeding.

In this respect, the barley mutant lines for erectoid character (ert-mutants) developed in SVALÖV, Sweden provide a very unique and ideal material to determine the usefulness of this type of diallel analysis. Diallel experiments can be set up with inbred lines involving two or three ert-gens with all possible combinations in the parents so that the sampling objection in relation to population question would cease. Moreover, the genetic background of this ert-character in barley is now well established following extensive studies by Persson and Hagberg (1969) and Persson (1969a, 1969b). These satisfy all the assumptions on which this diallel theory is based. Persson (1969c) in his diallel analysis with such barley mutant materials, involving two ert-genes, although he could not find interaction between non-allelic genes, however, gathered other information, as expected from conventional genetic knowledge.

This investigation presents a study on the effect of the failure of the following assumptions (a) random selection of parents; (b) no multiple allelism; and (c) no linkage in diallel analysis. Besides, results from diallel analysis with commercial varieties of barley which do not satisfy all the assumptions is presented for comparison with perfect diallel cross analysis, involving three ert-mutant genes, determines by comparison with

established knowledge from conventional genetic studies the usefulness of the Jinks-Hayman type of analysis in the breeding of selfpollinated crops. This also makes it possible to justify the accuracy with which the genetic system deduced from the parental and F_1 diallel cross data can be used for any prediction.

Materials and methods

This investigation was conducted in essentially four parts, each with a set of diallels and in a definite gene model to look into particular effects due to the following:

- (1) Three sets of diallels of which two sets, namely diallel I and V (Table 4a) each included two pairs of erectoid genes (recessive) and the third set (diallel VI - Table 3c) involved three pairs of ert-genes. The parents in the first set were Bonus (normal nutans variety), ert-a²³, ert-c³⁹ and the double recessive ert-a²³c³⁹. The four together by themselves, therefore, determined the complete population. The second set was similarly composed of four parents but with different ert-mutants determining a complete diallel with theoretically representable population. The parents were Bonus, ert-b², ert-i²⁷ and ert-b²i²⁷. All the ert-mutants except ert-b², used in the present investigation, were varieties introduced in Bonus barley. Ert-b² was introduced in Gull barley. Gull and Bonus, both nutans barley, are closely related (Borg, 1959). So the effect of the difference of mother barley variety would naturally be expected to be very small, if any. The third set of diallel included eight possible parents constituting the theoretical population that involved three pairs of recessive ert-genes affecting ear denseness. These parents were Bonus, ert-a²³, ert-c⁵⁹, ert-g⁸⁰, ert-a²³c⁵⁹, ert-a²³g⁸⁰, ert-c⁵⁹g⁸⁰, and the triple recessive ert-a²³c⁵⁹g⁸⁰. All the double and triple recessive parents (except ert-a²³c⁵⁹) in this investigation had been derived through preliminary observational selection of progeny of a cross between ert-a²³c⁵⁹ and ert-g⁸⁰ (for diallel VI) and other suitable single crosses. Each of these parents was confirmed through test crosses on the selections. Test crosses were conducted at the same time as the crosses (hybridization). The completed full diallels for the first two sets and the half-diallel for the third were analysed essentially in accordance with the method outlined by Jinks (1954) and Hayman (1954a, b). The results were expected to reflect on the utility and usefulness of the method and the need for such a system to the advantage of plant breeding. As three ert-mutants were involved in the third diallel sets, a better information about interaction of genes was expected. The two 4x4 diallel sets would provide a suitable comparison.
- (2) Excluding parents, one at a time, in the analysis of the 8x8 diallel studied, the importance of the assumption of random selection of parents was studied. This constituted the second experiment in the present investigation.
- (3) Three sets of 4x4 full diallel crosses (Table 4a), each involving multiple alleles, were carried out to study the effect of multiple

allelism on diallel analyses. The four parents in the first set were Bonus, ert-a³⁶, ert-c³⁹ and ert-a²³c³⁹. The second set had Bonus, ert-a²³, ert-c⁹⁷ and ert-a²³c³⁹ as their parents, while the third set included both ert-a³⁶ and ert-c⁹⁷ along with Bonus and ert-a²³c³⁹ as parents. The regular four parents' diallel which included Bonus, ert-a²³, ert-c³⁹ and ert-a²³c³⁹ and was mentioned under the first experiment, stood as a comparison against sets of multiple alleles. The results of this experiment (3) should be treated and described along with experiment (1) specially to compare it with perfect diallels of experiment (1) and reflect the difference from them due to involvement of multiple alleles in experiment (3).

(4) The fourth experiment dealt with sets of diallels (Table 4b) that included in one, parents that had partially linked ert-mutant genes, and in another, closely linked ert-genes. Bonus, ert-a²³, ert-m⁴⁰ and ert-a²³m⁴⁰ constituted the partially linked gene parents whereas Bonus, ert-a¹³, ert-d¹⁵ and ert-a¹³d¹⁵ built up the closely linked groups. Both the types of linkage were in repulsion and hence a large population, specially for a¹³d¹⁵, had to be grown to select for the double recessive parents. Crossing had to be spread out over two years to complete all possible crosses to constitute the half-diallel for the F₁s. Next year F₂s were grown in the field. They were subjected to diallel analyses to find the effect of correlated gene distribution on such a type of analysis.

For the 8x8 diallel parents 1 - 8 listed in Table 1 were crossed in all combinations, without reciprocals, giving a total of 36 crosses. In the present investigation the parents, as noted above, were dense ear mutants (ert-mutants) in barley. The mutant character common to all ert-mutants, is shorter ear internode length. The genetic background of these materials is extensively investigated; allelism has been well established, gene location studied and chromosome maps made (Persson and Hagberg, 1969; Persson, 1969a, 1969b; Hagberg, 1960; Hagberg, Gustafsson and Ehrenberg, 1958; Hagberg, 1959). Many ert-mutations were induced in the same original genotype, namely Bonus; and by choosing such non-allelic and unlinked mutant barley varieties, sets of these perfect diallel crosses were made which not only satisfied all the assumptions for a diallel theory but also included all possible combinations of genes in the parents.

Hybridization work started in 1969 and continued through the winter (1969-70) in the greenhouse to next summer in the field. Crosses were made between varieties in accordance with the diallel scheme including reciprocals and selfings for experiment (3) and without reciprocal for the rest. F₁s were grown in the field during summer 1971. Hybrid seeds were collected

sufficiently for all the diallels, except 3 crosses for 8x8 diallel where seed settings were poor and fell quite short of the requirement. The plants (F_1 s and selfed parents) were spaced 5 cm. in two rows 15 cm. apart and had a blank row in between each hybrid cross. These rows were in a field track 1.5 meters wide. Each cross was represented by a minimum of 10 plants in each plot; a minimum of 20 plants for the two replications per cross in a completely randomised block trial was grown in each case which included both selfed parents and F_1 s.

Measurements were recorded on individual plants after harvest, and the ear length character was evaluated as follows:
Density of the ear was defined as the total length in mm. of ten internodes starting at the base from spikelet (floret) no. 5 and ending spikelet no. 15 (Persson and Hagberg, 1969). The top two ears in each plant were selected for such measurements.

All the analyses of the characters and the methods used in this investigation followed the conventional method of diallel crosses given by Hayman (1954a, b). The analysis of variance of the diallel tables presented by Hayman (1954a) was used to estimate the variances of additive, dominance and maternal effects in all 4x4 full diallels. For the 4x4 and 8x8 half diallels the analysis of variance was due to Hayman (1954a), modified for the half diallel by Jones (1965), and the analyses involved data from parents and F_1 families for 8x8 diallel, but parents and F_2 families for 4x4 diallels. The basic notations of this paper follow Mather (1949) and Hayman (1954a, b).

Theory

The theory of a diallel cross, as defined by Jinks and Hayman (1953) and Hayman (1954b), between a number (n) of homozygous parents, the parameters for additive gene effects (D), dominance (H) and distribution of genes (F) are given by:

$$\begin{aligned} D &= 4 \sum uvd^2 & \text{(The notation used} \\ H_1 &= 4 \sum uvh^2 & \text{is that of Mather, 1949.)} \\ H_2 &= 16 \sum u^2 v^2 h^2 \\ F &= 8 \sum [uv(u-v)dh] \end{aligned}$$

where u and v are the frequencies of increasing and decreasing alleles respectively, and $u + v = 1$. The parameters are estim-

ated from the variation of parental lines, array variances, array covariances, and from the variation of array means around the overall mean. The diallel cross analysis permits two possible approaches. Equations of estimation can be set up and solved to obtain estimates of the parameters as above, whose genetic content is interpretable on the basis of diallel theory. Alternatively, the data can be used to construct graphs that can be interpreted in terms of the genetic control of the character under investigation. In other words, the contribution of a locus A,a to the family means in a p^2 diallel cross may be described in terms of the parameters u_a (proportion of parents that are AA), v_a (proportion of parents that are aa), d_a (additive phenotypic increment of the gene A,a). A number of first and second degree statistics can be calculated from the family means. The genetic content of certain of these statistics in terms of the above parameters can be shown to be as follows:

$$\begin{aligned} \text{Variance of parents} &= V_{OLO} = 4\sum uv d^2 \\ \text{Mean variance of arrays} &= V_{ILI} = \sum [uv(d^2 - 2\{u-v\}dh + h^2)] \\ \text{Variance of array means} &= V_{OLI} = \sum [uv(d - \{u-v\}h)^2] \\ &\quad (\text{around the grand mean}) \\ \text{Mean covariance of arrays} &= W_{OLOI} = 2\sum [uvd(d - \{u-v\}h)] \\ &\quad (\text{covariance of offspring on} \\ &\quad \text{to non-recurrent parents}) \end{aligned}$$

Here the subscript L refers to the diallel cross-mating system, and the subsequent number(s), beginning with zero for the parents, refer to the generations under considerations. In variances of individual measurements, the number preceding L is the same as that following, whereas in variances of means and in covariances, the number(s) preceding L refers to the generation(s) of the common parent.

It then follows from the diallel cross components of variance, as defined earlier, that

$$\begin{aligned} V_{OLO} &= D + E \\ V_{ILI} &= \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} F + [E + (n-1)E_1] / n \\ V_{OLI} &= \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} H_2 - \frac{1}{4} F + [E + (n-2)E_1] / n^2 \\ W_{OLOI} &= \frac{1}{2} D - \frac{1}{4} F + E / n, \end{aligned}$$

in which the additional term E = environmental variance of diallel cross family means, and n = number of parents or number of arrays. The stated theory of the diallel cross analysis (Jinks and Hayman, 1953; Jinks, 1954; Hayman, 1954a, 1954b) is based on the following assumptions:

- (1) homozygous parents
- (2) diploid segregation
- (3) no reciprocal differences
- (4) no epistasis (that is, no non-allelic genic interaction)
- (5) no multiple alleles
- (6) uncorrelated gene distribution and no linkage
- (7) no genotype-environment interaction.

The analysis of variance of the diallel table as presented by Hayman (1954a) estimates the variance of additive (a), dominance (b), and maternal effects (c) and (d). It is possible to subdivide the (b) item into parts (b_1), (b_2) and (b_3) measuring respectively the overall difference between parents and progeny, i.e., dominance, the consistency of the dominance effects over the lines, and finally any specific differences which might occur between parental and progeny means.

The analysis of variance was also used in this paper. The relationships between the components of variance of the diallel and the components of variance in the broader, more inclusive diallel analysis are as follows:

AOV	<u>Diallel analysis</u>
a	$D - F + H_1 - H_2$
b	H_2
b_1	h^2
b_2	$H_1 - H_2$
b_3	Residual
c	Maternal differences
d	Reciprocal differences not maternal

Since the analysis is invalidated to some degree by failure of any of the seven initial assumptions, either one or more than one of the following three broad, general tests could be

used to determine whether the assumptions would be fulfilled by the characters; (1) Analysis of variance of the quantity $(W_r - V_r)$, (2) analysis of the (W_r, W_r^-) regression, and (3) analysis of the (V_r, W_r) regression. V_r is the variance of the members of an individual array; W_r is the covariance of the members of an array with their nonrecurrent parents; and W_r^- is the covariance of the members of an array with the array means of their nonrecurrent parents. The third test is given

$$\text{by } t^2 = \frac{n-2}{4} \cdot \frac{(\text{Var. } V_r - \text{Var. } W_r)^2}{\text{Var. } V_r \cdot \text{Var. } W_r - \text{cov.}^2(V_r, W_r)}$$

with $n - 2$ degrees of freedom. The t testing the significance of regression indicates failure of the hypothesis. However, the present experiments were mainly motivated by the special reason that the chosen ert-mutants of barley are such unique and established varieties that they satisfy all of those assumptions, and also that types were available or could be created as desired to fail one or more of these specific assumptions of our interest. Following a failure of the test(s), the pinpointing of the offending assumptions may be difficult in some cases. Elaborate and additional experimentation is required to test the assumption of no genotype-environment interaction within location and years and no epistasis. When a trait exhibits a partial failure of the assumptions, estimates of the population parameters of that trait are still possible (Hayman, 1954b), although the estimates for such a trait are possibly less reliable than when all assumptions are fulfilled.

Validity of assumptions

Parental homozygosity and diploid segregation are assured from the history of self-pollination of the parents and from numerous reports from literature not only that nutans Bonus barley regularly forms 7 bivalents at meiosis but also that inheritance in this species is uniformly disomic.

The absence of reciprocal differences was established by proper diallel analysis (Persson, 1969c) and by earlier observation from the data that the value of an F_1 does not depend

on the direction of the cross in these varieties of barley. In the present investigation simultaneous experiments were set up to look into this aspect. Relevant experimental materials to confirm the lack of reciprocal differences in the parental ert-varieties gave identical information as reported earlier by Persson (1969c).

The data also indicated that the assumption of absence of genotypic-environmental interaction within locations and years was always valid (Persson and Hagberg, 1969), especially as block means. The present investigation also had borne out the truth.

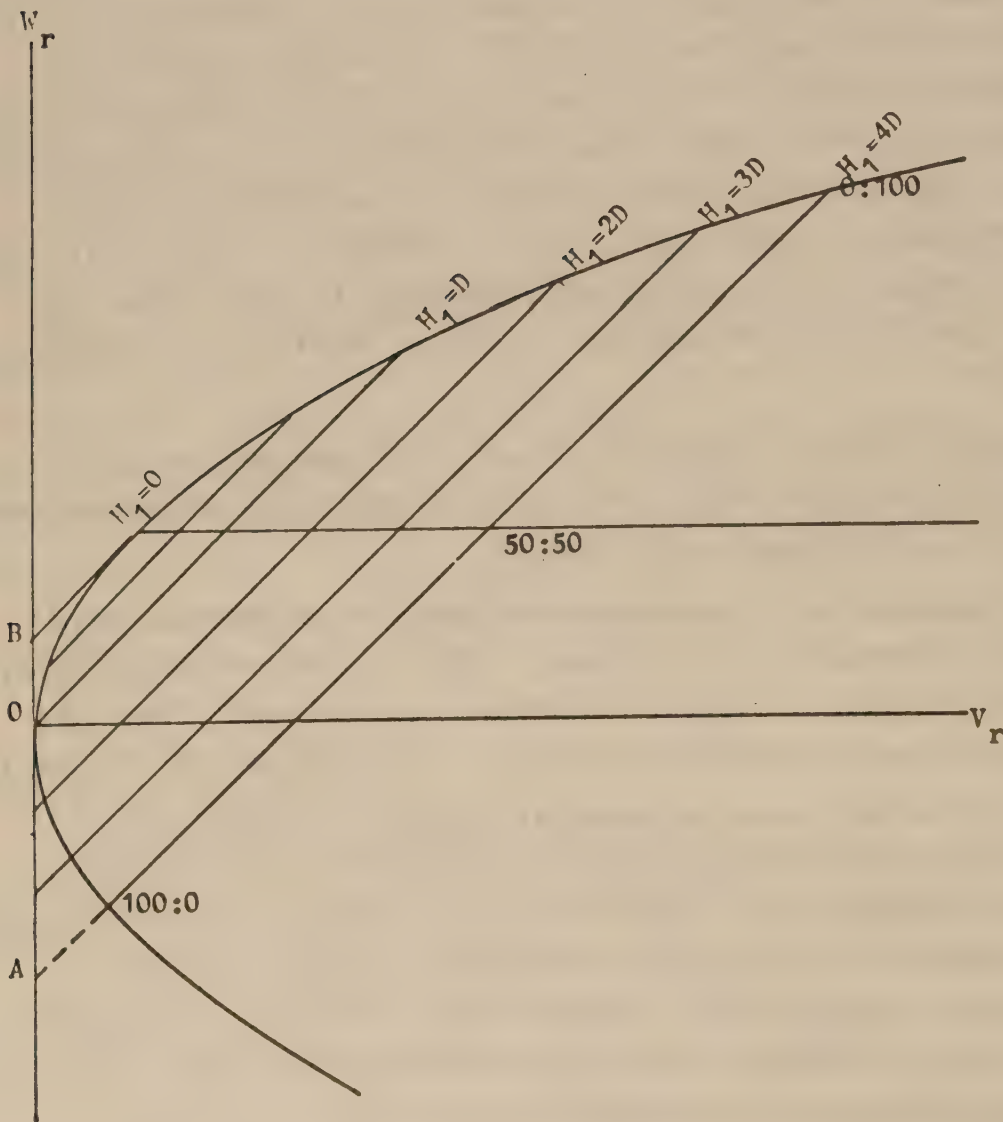
Wide use of the materials in different experiments and the real methods of introducing the non-allelic ert-mutants in the mother barley variety Bonus and their subsequent evaluation (Persson and Hagberg, 1969) have borne out the assurance that the chosen materials for perfect diallel are all parents that suffer no interallelic gene interaction, multiple alleles or non-random gene distribution. On the other hand materials were assuredly known which could be handpicked to fail these conditions specifically where such failures were to be experimented against.

Hayman (1960a), however, showed that the measure of dominance is not seriously disturbed by multiple allelism, and that it is unimportant until the F_2 .

The assumption of uncorrelated gene distributions may be tested (Crumpacker and Allard, 1962) by the ratio, $\frac{1}{4} H_2/H_1$. This ratio in case it did not differ significantly from the expected for any character would prove the assumption to be true.

In a diallel cross experiment dominant relationships can be graphically represented in terms of V_r , the variance of all the offspring of the r th parent, and W_r , the covariance between these offsprings and their nonrecurring parents. For a diallel cross with a certain value of H_1/D , the points (V_r, W_r) are distributed along a corresponding straight line of unit slope inside the limiting parabola, $W_r^2 = V_r V_{0LO}$.

This is one of the full sloping lines in the following diagram. If the continued line cuts the W_r axis in A, and if the parallel tangent to the parabola cuts it in B, then the line is determined by $AB/OB = H_1/D$. The position of (V_r, W_r) on the line reveals the relative proportions of dominant and recessive genes in the r th parent. Fully recessive parents correspond to points at the upper end of the sloping line on the part of the limiting parabola labelled 0:100, and completely dominant parents, to points at the lower end on the part labelled 100:0. With no dominance all the points coincide at $(\frac{1}{4} D, \frac{1}{2} D)$, that is $H_1 = 0$ in the diagram.



The parabola ($W_r^2 = V_p - V_r$) marks the limits within which the points (V_r, W_r) should lie. As the regression of (V_r, W_r) agrees with a slope of 1 (one) the gene system can be deduced to be additive without the complication of gene interaction. If dominance of the genes is complete the line with slope $b = 1$ would pass through the origin 0. In the case of over-dominance the regression line would cut the W_r axis below the origin, and in the absence of dominance the points would cluster about the position where the slope of the parabola is +1. The position of this line, being near to that of a tangent to the parabola, indicates little dominance. The order of the array points on the line indicates the distribution of dominant and recessive genes among the common parents of the arrays. The points of intersection of the line and the parabola are the positions which would be taken by an array, the common parents of which contained all the dominant or recessive genes segregating in the group of crosses (the top dominant nearest the origin). With no dominance all the points coincide at $H_1 = 0$ ($\frac{1}{4} D, \frac{1}{2} D$), in the diagram.

The methods of Hayman and Jinks obtain sufficient information from the grouping of crosses from a diallel set into arrays rather than by using many families from one cross. In this context an array is defined as one variety and all the crosses involving it. This analysis gives, among other things, information about the average additive effects of the genes, about the effects of heterozygosity, about the dominance of the genes in each parent, and about gene interaction. High manifestation of a character in a cross can thus be attributed either to heterozygosity (unfixable on inbreeding), to additivity of gene action or to non-additivity of gene action, i.e., to interaction if the non-additivity is between loci or to dominance relationships if the non-additivity is within loci. It can also be decided, in those cases where dominance relationships are effective, whether the high manifestation is due to dominant genes, to recessive genes or to a balanced grouping of dominants and recessives. Furthermore the analysis should demonstrate whether any of the varieties used as parents

contains the complete complement of dominant or recessive genes available in the parents used. If the high manifestation of a character is due to the possession of either dominant or recessive genes it becomes possible to assess the chances of obtaining selections which will transgress the parent which contains most dominant or recessive genes.

The component, E is an estimate of the parental environmental variation while E_1 is the corresponding estimate of the F_1 environmental variation. The remaining genetic components are D , F , H_1 , and H_2 . D is the additive genetic variance parameter which may also include a portion of the additive x additive epistatic variance. H_1 and H_2 are dominance genetic variance parameters which may include the dominance genetic variance proper, dominance x dominance epistatic variance, and additive x dominance variance as well as the portion of the additive x additive variance not included within D . F is an indicator of the relative frequency of dominant and recessive alleles in the parents and may take sign; since $F = \sum [uv(u-v)dh]$, its sign depends on the sign of $(u-v)h$. The other parameters are expected to be positive. A negative F value results if there is an excess of recessive alleles in the parents or if no genes exhibit dominant effects (Crumpacker and Allard, 1962). Estimates of these four parameters are obtained by solving (successive substitution) the equations which follow, where n equals the number of parents.

$$(1) \text{ Variance of the parents} = V_{OLO} = D + E$$

$$(2) \text{ Mean covariance of arrays} = W_{OLOI} = \frac{1}{2} D - \frac{1}{4} F + E/n$$

$$(3) \text{ Mean variance of arrays} = V_{ILI} = \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} F + [E + (n-1)E_1]/n$$

$$(4) \text{ Variance of array means} = V_{OLI} = \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} H_2 - \frac{1}{4} F + [E + (n-2)E_1]/n^2$$

The estimates of V_{OLO} , W_{OLOI} , V_{ILI} , and V_{OLI} were obtained from the diallel table.

The method of analysis permits an interpretation of the regression of array covariances on array variances in conformance to the basic assumptions. Theory requires that, with each gene independent of all others in its action, the variances and covariances of arrays (V_r, W_r) of a set of diallel crosses with a given value of dominance (H_1/D) be distributed along a straight line of unit slope inside the limiting parabola, $W_r^2 = V_r V_{OLO}$. Thus $W_r - V_r$ values are constant over arrays. Since D and H_1 are weighted sums of d^2 and h^2 , respectively, the ratio H_1/D allows an estimate of the mean degree of dominance.

Genetic analysis of diallel crosses

The quantity $W_r - V_r$ is equal to $\frac{1}{4}(D - H_1)$ and is expected to be constant over all arrays provided the basic assumptions of the diallel cross analysis are valid and there is no environmental effect (environmental effect = 0). Now, because $\frac{1}{4}(D - H_1)$ does not vary with arrays under these conditions, $W_r = \text{constant} + V_r$, and the regression of W_r upon V_r is a straight line of unit slope. When $V_r = 0$, $W_r = \frac{1}{4}(D - H_1)$. W_r intercept is, therefore, an indicator of the average degree of dominance in the experimental materials on the (V_r, W_r) graph. When $H_1 < D$, the dominance is partial and W_r intercept is positive. With overdominance, $H_1 > D$, and the W_r intercept is negative. When there is no dominance, $H_1 = 4 \sum uvh^2 = 0$ and $F_r = \pm 8 \sum uvdh = 0$, so that

$$\begin{aligned} V_r &= \frac{1}{4} D + \frac{1}{4} H_1 - \frac{1}{4} F_r = \frac{1}{4} D \\ W_r &= \frac{1}{2} D - \frac{1}{4} F_r = \frac{1}{2} D \\ \text{or} \quad V_r &= \sum uv(d \pm h)^2 = \sum uvd^2 \\ W_r &= 2 \sum uvd(d \pm h) = 2 \sum uvd^2. \end{aligned}$$

In this situation all points on the (V_r, W_r) graph are estimates of the single point $W_r = 2 V_r$, and there is no regression. Hence the graph (V_r, W_r) gives test of significance for the presence of dominance ($b \neq 0$) and the average degree of dominance (sign of a), where $\underline{b}$ is the slope of the regression line and $\underline{a}$ is the W_r intercept.

From the genetic components, D , H_1 , H_2 , F , and h^2 , the following genetic parameters were further estimated. Some of the important estimators that could be derived from the diallel cross parameters, are listed in Table 7, along with means and standard errors. Most of these estimators are ratios and their errors are approximations.

H_1/D is an estimator of the average degree of dominance, since $\frac{H_1}{D} = \frac{\sum uvh^2}{\sum uvd^2}$. It is weighted in favour of genes which have both alleles

represented equally in the parents, i.e., $u_a = v_a = \frac{1}{2}$. H_1/D is also weighted in favour of genes or closely linked blocks of genes, with large effects. With average partial dominance, H_1/D is expected to fall within the range 0 - 1. The quantity $\sqrt{H_1/D}$ is a weighted measure of the average degree of dominance at each locus. Another estimate of average degree of dominance could be obtained from the ratio $\frac{V_{ILI} - E}{W_{OLOI} - E/n}$. This is a

weighted estimator in the same sense as H_1/D .

Since $\bar{F}_1$ and $\bar{P}$ are the over-all F_1 parental means, the sign of $\bar{F}_1 - \bar{P}$ was an indicator of the average direction of dominance.

The quantity $H_2/4H_1$ is an estimator of the average frequency of negative versus positive alleles in the parents. Since $\frac{1}{4} \frac{H_2}{H_1} = \frac{\sum u^2 v^2 h^2}{\sum uvh^2} = \bar{u}\bar{v}$, it has a maximum value of $\frac{1}{4}$ when $\bar{u} = \bar{v} = \frac{1}{2}$. If the negative and positive alleles were not distributed equally among the parents, $\bar{u}\bar{v} < \frac{1}{4}$. If the "h-effects" of genes, or closely linked blocks of genes, were unequal, the genes with large "h-effects" would have been favoured. Genes with both alleles represented equally in the parents would also receive more weight. It would be noted that no information was provided about genes that had no dominance effect.

The parameter $F = 8[uv(u - v)dh]$. The sign of this parameter depends on the sign of $(u - v)h$. If no genes exhibited dominance effects or if the recessive and dominant alleles of each gene were distributed equally among the parents, $F = 0$. F would be positive if there was an excess of dominant alleles or of dominant genic effects. But an excess of recessive alleles or of recessive genic effects would make F negative. Hence the sign of F was an indicator of the relative frequencies of dominant and recessive alleles in the parents. When the h effects of different genes were unequal, the sign of F would be weighted in favour of genes with large h effects.

Mather (1949) has described an effective factor as the smallest unit of hereditary material that is capable of being recognized by the methods of biometrical genetics. It can be a

group of closely linked genes, or, at the lower limit, a single gene. In a diallel cross,

$$K = \frac{(\text{over-all progeny mean} - \text{parental mean})^2}{\frac{1}{4} H_2}$$

$$= \frac{(\sum uvh)^2}{\sum u^2 v^2 h^2},$$

where K = number of effective factors. The value of K will be underestimated unless the h effects of all the genes are equal in sign (direction) and size, and the distribution of the genes is uncorrelated (Mather, 1949; Jinks, 1954). Here also the analysis gives no information about genes that have no dominance effects.

$$\frac{(4DH_1)^{\frac{1}{2}} + F}{(4DH_1)^{\frac{1}{2}} - F} \quad \text{estimates the ratio of the total number of}$$

dominant to recessive genes in all the parents. Since parents containing the most dominant homozygotes of genes controlling the characters in question, produce offspring with the least variation amongst themselves and the least covariance with their non-recurring parents, the relative values of $W_r + V_r$ provide an estimate of dominance order of the lines involved in the diallel crosses.

The ratio V_{ILI}/W_{OLOI} also measured dominance, but on a different scale from that of H_1/D , but when $u = v = \frac{1}{2}$, H_1/D and V_{ILI}/W_{OLOI} may be converted to the same scale by the transformation of V_{ILI}/W_{OLOI} to $2(V_{ILI}/W_{OLOI} - \frac{1}{2})$ as shown by Jinks (1954).

Results

If the diallel cross conforms to the assumptions listed earlier $W_r - V_r$ is constant. Heterogeneity of $W_r - V_r$ thus would indicate nonconformance to the model. Because of the replications in this study, it was possible to analyse the variance of $W_r - V_r$ to test for failures of the hypotheses. Table 5 gives these results. Standard errors for the diallel

analysis were calculated by use of the table of covariance matrix and gives the approximate standard errors of the genetic components of the diallel analysis.

When significant dominance was found, the correlation between y_r (parents) and $W_r + V_r$ was calculated; if this was significant, the theoretical limits of selection among genes exhibiting dominance could then be calculated.

In the analyses of variance of $W_r - V_r$ for the ear length character (table 5) diallel I, II and V showed no significant variation among the n lines. From the standpoint of conformity to the model employed here it, therefore, appeared that the analyses of the character were valid. However, diallel III + IV proved to the contrary as should have been expected because of their involvement of multiple alleles. From the same point of view diallel II was an exception. The reasons are evidently the very little difference in properties of the two alleles a^{23} and a^{36} and absence of any evident interallelic interaction. Table 2 shows the ear length measurements in mm of Bonus and other ert-mutant varieties of barley (Persson and Hagberg, 1969).

Table 6 shows the mean square values for the sources of variance in the analysis of variance for ear length in each of the five diallels studied. Each mean effect was tested against a pooled error mean square with 15 degrees of freedom. Bartlett's test had shown the six individual error variances B_a to B_d to be homogeneous in each diallel case,

$$\text{Diallel I} - \chi^2_{(5)} = 5.96, \quad P = 0.4 - 0.3$$

$$\text{II} - \chi^2_{(5)} = 3.82, \quad P = 0.6 - 0.5$$

$$\text{III} - \chi^2_{(5)} = 5.26, \quad P = 0.4 - 0.3$$

$$\text{IV} - \chi^2_{(5)} = 4.06, \quad P = 0.6 - 0.5$$

$$\text{V} - \chi^2_{(5)} = 3.95, \quad P = 0.6 - 0.5$$

Component a was highly significant in each case. This component measures only additive variation when dominance is absent. Component b, the dominance component was also highly significant in each case. The (b) main effect had been split into its component parts; in genetical terms (b_1) is taken as a measure of the mean dominance deviation, (b_2) as a further dominance deviation due to asymmetrical gene distribution, and (b_3) as an estimate of any specific interaction (Hayman, 1954a). Component b₂ in the analysis of variance was not significant in diallel V and just significant in diallels I + II but highly significant in diallels III and IV; thus symmetry of gene frequencies for this character having significant dominance was indicated in diallel V but not in I + II (component b_2 is zero when no dominance exists). Significance of b_2 in the two diallels III and IV showed a condition of gene asymmetry in all of the parents. This is also a natural consequence of interaction of

of multiple alleles introduced into these diallels.

Some maternal effects just on the limit of significance showed to be associated with the character in diallel V. It is, however, conceivable that such a result could have been due to abnormal or reduced phenotypical manifestation of materials in four of the diallel crosses grown under greenhouse conditions to substitute the reduced field crop harvest. However, all the other diallels revealed no trace of maternal effect. Similarly the block interaction in all cases was almost untraceable, which means that environmental interaction with phenotypes was untraceable.

Among the components (Table 7) estimated by the broader diallel analysis, the additive component D was highly significant. Dominance components H_1 and H_2 were both significant in all the diallels. The overall measure of dominance was 0.76, 0.75 and 0.79 in diallels I, II and V respectively, while III and IV showed values of 1.13 and 1.22 respectively. Thus partial dominance was revealed in the former cases while the latter group of two diallels manifested overdominance to some extent.

The proportion $H_2/4H_1$ estimates the product $u_i \times v_i$. The notations u_i and v_i refer to the frequencies of parents with positive and negative homozygotes, respectively, at the locus "i". When these frequencies are equal, $u_i v_i = \frac{1}{2} \times \frac{1}{2} = 0.25$. For diallel I and II these figures are 0.26 and 0.25 respectively. These findings contrasted the results already shown by component b_2 in the analysis of variance. So also, contrary to expectation, diallel V showed this value as 0.11 which revealed asymmetry in the parents for ear length character. Although there were some evidences of asymmetry in the estimates of the product $u_i v_i$ and the ratio of dominance to recessive genes in diallel V, the fact that no such asymmetry was detected in the analysis of variance of the diallel or in the analysis of variance of $W_r - V_r$, indicated that there were insufficient biases to distort the analysis. On the other hand, findings of value of 0.22 in each of diallels III and IV confirm the results already shown by component b_2 in the analysis of variance, that is to say, $\bar{u} \neq \bar{v} \neq \frac{1}{2}$ for the character. When the alleles were not distributed equally among the parents, they were correlated to some degree and the quantity was less than $\frac{1}{4}$. Consequently the assumption of uncorrelated gene distribution in the parents is fulfilled as mentioned earlier, if the quantity was not significantly different from 0.25. From table 7, it could be found that $H_1 > H_2$ in both the diallels, i.e., the positive and negative alleles at these loci are not in equal proportion in the parental varieties.

Now the proportion $[(4DH_1)^{\frac{1}{2}} + F] / [(4DH_1)^{\frac{1}{2}} - F]$ should be unity if the total number of dominant genes in all the parents is equal to the total number of recessives (assuming equality of gene effects). Unity was approximated by the 0.95 value obtained. All the values here except in diallel III could be taken as close to unity, implying proximity between the numbers of dominant and recessive alleles in the parents. The diallels III and IV with values 1.35 and 1.24 respectively, were affected by complementary gene interactions, since the values were higher than would be expected in a diallel showing no interaction.

The number of groups of genes (or, quite possibly, number of genes) which exhibit dominance to some degree and which

control ear denseness is estimated by h^2/H_2 (or $\frac{(\bar{F}_1 - \bar{P})^2}{\frac{1}{4} H_2}$),

for which values of 1.98, 2.10, 2.52, 2.73 and 5.62 were obtained (again assuming equality of gene effects). The first two values indicate that perhaps two such groups were present whereas three such groups were possibly indicated for ear length in diallel III and IV. The number of effective factors in diallel V (5.62) revealed a value which remained somewhat obscure, without simple explanation. It must be emphasized that these values usually underestimate the number of groups, since positive and negative effects of dominance genes cancel one another. On the other hand, dominance could be sufficiently unidirectional to cause h^2 to be significant, so perhaps these estimates may approach the actual number.

The order of dominance of the parents, determined by $(W_r + V_r)$ was 1 (10) 2 (12), 1 (10) 9 (12), 1 (11) 2 (12), 1 (11) 9 (12), 1 (14) (13) (15) respectively in diallels I, II, III, IV, and V.

The correlation of $(W_r + V_r)$ and y_r (parents) were - 0.9805*, - 0.9862*, - 0.8961, - 0.9388 and - 0.9978** respectively in the I to V diallels. Since $(W_r + V_r)$ values were correlated with the recessive homozygotes, dominance and

in three of them, significant dominance in a positive direction = lax ear (greater "ear length") was indicated, that is, most of the dominant genes had positive effects (lax ear). Low level of correlation between $(W_r + V_r)$ and y_r in diallel III and IV would mean that some of the genes showed dominance in a positive direction for the character (lax ear) while eventually some acted in the negative direction for the character (dense ear). But this interpretation would be subject to modification because of the presence of multiple alleles.

From the values of $(D - H_1)$ in diallels I, II, and V it followed that the additive genetic variances were greater than the dominance genetic variances for ear length as was also quite evident from their analyses of variance, noted earlier. On the other hand in cases of diallels III and IV dominance genetic variances showed greater values than additive genetic variances, both for $(D - H_1)$ and in analysis of variance for the two diallels.

The components of variation (Hayman, 1954a) and their proportions (upon which the graphical treatment was based), reflected, and in part, summarized, the results of the graphical analysis.

Negative values of F in diallels I and II denoted an excess of recessive alleles while an excess of dominant alleles was indicated in diallels III, IV, and V. Graphically this was traceably apparent.

Graphical analysis

The results of the homogeneity test of $(W_r - V_r)$ (Table 5) indicated that the Hayman assumptions (1954b) were adequate for diallels I, II, and V but failed for diallels III and IV as was expected. However the single diallels of the replications indicated valid t^2 -test of Hayman (1954b) showing t values nonsignificant for diallels III ($P = 0.5 - 0.4$) and IV ($P = 0.3 - 0.2$). Therefore, it is permissible to adopt Hayman's method to draw the (V_r, W_r) graph (Fig. 1, 2, and 5) for diallels I, II, and V. It was also possible to draw (V_r, W_r) graphs for diallels III and IV (Fig. 3 and 4) to look

into the behaviour of the regression lines and the effects due to the multiple alleles. The values of V_r , W_r , V_p and $(W_r + V_r)$ for these diallels were given in Table 7a. Though diallel II also included multiple alleles in ert-a³⁶ along with ert-a²³c³⁹ and allele AA of the mother variety Bonus, the effect due to their phenotypic difference in "ear length" (Table 2) was so slight, and interallelic interaction so minor, if any, that the ultimate disturbing effect on the diallel analysis was almost negligible or nil. The results, therefore, were completely in line with the perfect set of diallel I or V. On the other hand ert-c⁹⁷ (Table 2) had a differential phenotypic effect on its own allele c³⁹. This alone, in diallel III, or together with a³⁶ in diallel IV, had a disturbing effect on the diallel analysis showing interallelic interaction that evidently showed on the graph by its movements to the right, and an increase on the dominance effect (Fig. 3 and 4).

As depicted in Fig. 1, 2, and 5 for the character "ear length", the W_r s were significantly correlated to the V_r values, giving significant slopes, $b = 0.995 \pm 0.053$ ($P < 0.01$) in diallel I, $b = 0.976 \pm 0.022$ ($P < 0.001$), and $b = 1.019 \pm 0.061$ ($P < 0.01$) and these slopes were not significantly different from the unit slope ($P > 0.7$, $P \approx 0.3$, and $P > 0.7$ respectively for diallels I, II, and V). The parabola, $W_r^2 = V_p V_r$, delimits the area in which co-ordinate (W_r , V_r) array data occurred. The line of unit slope (45° angle) through the origin was the line of complete dominance. As the regression line of unit slope (45° angle, but passing through $\bar{W}_r$, $\bar{V}_r$) moved upwards to the left (not drawn in the graphs) of the line of unit slope in all three cases, decreasing partial dominance was manifested. The lines represent average tendencies over all arrays (F_1). The results here would indicate the existence of additive and partially dominant genes among the parental gene combinations; but there was no genic interaction.

The movement of the regression line downwards to the right denotes increasing dominance and, thus, when the intercept between the regression line and the W_r ordinate is below the origin there are indications of overdominance. With interaction

between the parental genes the slope of the regression line would give a significant deviation from unit slope ($b < 1$). In diallels III and IV involving multiple alleles the regressions became less significant, the slopes were probably different from unit slope ($P \approx 0.1$ in both). Partial dominance in diallel II, having the allele a^{36} was slightly less in dominance level compared to diallel III with its allele c^{97} . This increase in partial dominance had almost turned to complete dominance with inclusion of both the alleles a^{36} and c^{97} in the diallel IV. Moreover in both III and IV there were evident downward movements of the regression lines from that of unit slope which denoted an interaction between parental alleles. In fact, both the regression lines of unit slope through $\bar{W}_r$, $\bar{V}_r$ in the two diallels III + IV respectively, intercept the W_r ordinate below the origin, thereby indicating tendencies towards over-dominance. Therefore, the results could be interpreted as indicating the presence of interallelic interaction, particularly complementary interaction between parental alleles in the $W_r V_r$ graphs for mean values over blocks, showing also an apparent tendency of overdominance which was no doubt a spurious result of interaction.

Again it could be found here that allele a^{36} in diallel II had the negligible change of allelic effect in the parents. The regression showed that allele a^{36} almost took the same values as those of allele a^{23} . On the other hand in diallel IV, a^{36} reacted with comparatively much less recessive effect.

The graphical analysis of the full 4×4 perfect diallels I and V (16 crosses each) is given in Fig. 1 and 5. Here the actual regression lines and the lines of unit slope through the origin have been drawn. The regression coefficients were not significantly different from unity ($P > 0.7$ in both). In diallel I the arrays were separated into two evident groups more or less to the two distal ends of the regression line, denoting strong dominant and recessive alleles. Of the two groups again, array 1 (Bonus) occupied the extreme lower end and array 12 (ert- $a^{23} c^{39}$) the extreme upper end of the regression line nearest the part of limiting parabola, denoting parent with all or most dominant genes and all or most recessive genes respectively. Array 10 (ert- c^{39}) and 2(ert- a^{23}) indicated excess of dominant and recessive effects respectively.

It is interesting to note that in diallel V the four array points formed three distinct groups; one (array 1 - Bonus) near the lowest end of the regression line, at the point of interception with the limiting parabola, denoting all dominant genes, and another (array 15 - ert- $b^{27} i^{27}$) near the uppermost end of the regression line at the point of interception with the limiting parabola, denoting all recessive genes. The third group comprising

array 13 (ert-b²) and array 14 (ert-i²⁷) were at or below the point of interaction ($\bar{W}_r/\bar{V}_r$), denoting, respectively, about equal proportion of dominant and recessive alleles. The regression line is highly significant and shows partial dominance. That an excess of dominant alleles tended to place an array at a point of low W_r , low V_r would be clear if it was remembered that a dominant allele, contributed by the recurrent parent of an array, gave a consistent dominance in all hybrids, thus resulting in $W_r = 0$ and $V_r = 0$. The degree of dominance (Table 7) could be estimated directly by visual inspection of the graph from $(AB/OB)^{\frac{1}{2}}$. These values were 0.76 and 0.80 for the two diallels I and V respectively. The estimates for the same, as determined by $(H_1/D)^{\frac{1}{2}}$ were also 0.76 for the former and 0.79 for the latter.

These two perfect diallels (I and V), as expected, displayed a classic set of results that closely satisfied the theoretical expectations for the diallel analysis. The theory of diallel crosses (Hayman, 1954b) stated that the parental measurement, y_r was closely correlated with the number of positive homozygotes in the parent while $(W_r + V_r)$ was correlated to the number of recessive homozygotes. Standardized deviations of y_r and $(W_r + V_r)$ were computed for "ear length", using the formula, $(x_i - \bar{x})/s$, where x_i was the value of the individual parent, $\bar{x}$ the mean of the parents and s the standard deviation. The results were put graphically in Fig. 1B - 5B. For values of $(W_r + V_r)$, "plus" denoted recessive, and "minus", dominant. For values of y_r , plus denoted long (lax) ear length, and minus, short (dense) ear length.

The association of short (dense) ear with recessiveness and of long (lax) ear with dominance was consistently borne out in the experiment here to conform to the real genetic situation. There were remarkably high negative correlations.

The graphical analysis given in Fig 1, 2 and 5 showed a remarkable relation between degree of excess of recessive genes in the parents (Table 2) and denser ear (length) with the ascent along the regression line. The positions of all arrays were almost on the regression line, indicating no genic interaction. The ert-c⁹⁷ was the only array that consistently showed positional upsets along the regression line in both the diallels III and IV in which multiple alleles were involved. Instead of showing an excess of recessiveness, there was for this array a shift towards an excess of dominance. This shift was also reflected in the standardized deviation data shown graphically in Fig. 3B and 4B. This changed behaviour from expected

recessive- to dominant gene excess had been accompanied by less increase in ear length in array c^{97} ; it remained deeper on the minus side than either array a^{23} or a^{36} . Strong correlation is evident in diallels I, II and V from the distribution of coordinate points in a marked linearity, with order of dominance and recessiveness quite in agreement with their (W_r, V_r) graphs. Only the point for c^{97} in both cases fell into the dominant, dense ear quadrant.

Though the correlation coefficients did not reach significance in these two diallels (III, IV) still a simple relationship between positions on the regression line and parental genotype could be found.

That no significant correlation was found between y_r , the mean of the common parent, and $(W_r + V_r)$ in the two diallels indicated also that dominances were not unidirectional (about equal proportions of dominant genes were positive and negative). It is, however, more likely that in these cases non-significance of the correlation coefficients for the co-ordinate points in spite of their numerically high values (-0.8961 and -0.9388 respectively in III and IV), was a consequence of the small number of parents involved.

The third set of diallel was a half diallel (36 crosses) involving 8 parents which had all possible combinations (genotypes) from 3 *ert*-genes determining dense ear character. The data on ear length, average of two replicates, were given for the arrays (8 parent half diallel) in Table 3 c (parental values = the values for selfing, along the diagonal). Table 3 a-b shows the same values respectively for the two replicates. The half diallel involved the 8 parents used as both male and female plants but without reciprocals. Here the analysis of variance was according to Hayman (1954a), modified for the half diallel by Jones (1965).

This analysis partitioned phenotypic variance into genetic and environmental components. It also separated genetic variance into additive effects (those fixable by selection) and non-additive effects and further detected the presence or absence of dominance and non-allelic interactions.

The F_1 -trials showed highly significant variance ratio for ear length character when the 36 populations were compared (by "populations" was meant the eight parents and the progenies of their 28 crosses). The analysis of variance of F_1 -trials was presented in Table 8 b. The analysis of variance for the diallel on the values for each replication was performed separately at first. The results were highly consistent and since there was no block difference (effect), consequently the analysis was repeated, using mean values over blocks (2 replications). The results for these analyses of variance are given in Table 8 a. The results from the two replications showed a remarkable similarity.

The interpretations of the results shown in Table 8 a were straightforward. The significance of (a) showed genetical variation amongst the parental varieties. The partitioning of dominance effects at some of the loci comprised 3 components b_1 , b_2 and b_3 . While the significance of (b_1) showed that the dominance is largely unidirectional, the significance of (b_2) implied asymmetry in the gene distributions amongst the parents. The significance of (b_3) on the other hand implied residual dominance effect that meant non-additive variation from other causes. Finally, there was no evidence (Table 8 b) that the difference in environment between the blocks (replications) had caused any variation in the character (ear length). The progeny mean being greater than the parental mean (from b_1) indicated that the dominance was in the direction of lax "ear length".

Regression analysis:

The t , testing the significance of regression for the homogeneity of ($W_r - V_r$), showed in the three diallels ($t > 0.5$ in each) that the corresponding diallel cross conformed to the Hayman hypothesis (1954b). It was, therefore, possible to draw the (V_r , W_r) graphs (Fig. 6-, 6 a- and 6 b-A) and to make estimations of the various genetical components. The results were given in Table 11. The values of V_r , W_r , V_p and ($W_r + V_r$) were presented in Table 8 c.

The information from the regression analysis was remarkably

in conformity over the two replications (Fig. 6 a- and 6 b-A). The graphical analysis based on means, averaged over two replications showed (Fig. 6-A) strong linearity in array distribution with the-usual reflections (similar to single diallels): dense ear arrays have an excess of recessive genes and lax ear arrays have an excess of dominant genes. The W_r , V_r graph for mean values over blocks was shown in Fig. 6-A. The joint regression coefficient over two blocks was highly significant but was not significantly different from unit slope ($P > 0.3$).

Each replication, diallel VIa and VIb respectively, gave uniformly high significant regression values $b = 0.9313 \pm 0.0812$ ($P < 0.001$) and $b = 0.8731 \pm 0.1191$ ($P < 0.001$) respectively. Both the slopes were not significantly different from the unit slope ($P > 0.4$ and $P > 0.3$ respectively). This indicated that only additive and dominant effects existed between the parental gene combinations and that genic interactions did not exist. The intercept of the regression lines on the W_r axis indicated uniformly in all the three diallels more or less to the same extent a partial dominance quite close to complete dominance. The passing of the regression line through the origin in each case proved a strong tendency towards complete dominance in the parents. The points of intersection of the line and the parabola were the positions which would be taken by an array, the common parent of which contained all the dominant or recessive genes segregating in the group of crosses, the complete dominant nearest the origin. Array 1 and 8 parents occupied extreme positions near intersections consistently in each diallel, the former a position nearest the origin and the latter the extreme recessive position. It could be said that parent 1 got all the dominant genes and parent 8 all the recessive genes which would agree perfectly to the actual situation in the two parents. Ascending the regression line, arrays occurred having increasing proportions of recessive alleles. Recessive alleles permitted increased variability and larger variances. The relative position of arrays along the line showing their order of dominance were consistently

the same in all the three diallels. The three arrays with their single recessive common parents 3, 4 and 2 respectively, took the lower positions along the regression lines in that order, showing an excess of dominant alleles. On the other hand, arrays 7, 6 and 5 with their double recessive common parents took upper positions along the line in that order showing an excess of recessive alleles. The graphical analysis, therefore, revealed completely the known genetic composition of the parents and their expressed function. The technique was sensitive as to array expression of average degree of dominance and gave no indication of non-allelic interaction.

Very high correlations in all the three cases (Fig. 6 a-, 6 b- and 6-B) between y_r , the parental measurements, and $(W_r + V_r)$, the order of dominance of the parents, were found. This indicated that dominance was unidirectional. The relation of quadrants to recessiveness and dominance and to lax and dense ear is shown in the figures. The distribution of co-ordinate points and the correlation coefficient showed a very close negative association between dense ear (shorter ear length) and an excess of recessive alleles, and between lax ear (longer ear length) and an excess of dominant alleles. The array distributions of Fig. 6 a-, 6 b- and 6-A were of course reflected in the vertical (order of dominance) distribution of parent-array points in Fig. 6 a-, 6 b- and 6-A respectively.

However, an additional piece of information could be extracted from here in that the ear length (horizontal distribution, based on parental values) was associated with order of dominance so that dense ear was associated with recessiveness and lax ear with dominance. The order of dominance of the parents obtained from $(W_r + V_r)$ was 13427658.

The results of the genetic analysis for ear length for mean values over blocks (diallel 6) were given in Table 11.

The mean degree of dominance was given by $(H_1/D)^{1/2}=1.00$, which value indicated complete dominance in the F_1 . The degree of dominance was also estimated by using $(AB/OB)^{1/2}$

and $(A^1B/OB)^{1/2}$ estimated from the regression analysis (Fig. 6-A), (the latter was estimated from regression line of unit slope through V_r, W_r). The values were estimated 0.90 and 1.0 by $(AB/OB)^{1/2}$ and $(A^1B/OB)^{1/2}$ respectively. The difference in the latter two values is due to the fact that the environmental variation had been eliminated in $(A^1B/OB)^{1/2}$.

The ratio of positive to negative alleles at loci exhibiting dominance, was $H_2/4H_1 = 0.23$. This indicated closeness to symmetry. It was however not completely in agreement with the results obtained from the analysis of variance (Table 8 a), in which (b_2) was found significant, indicating gene asymmetry. Also Table 11 shows that H_1 was slightly greater than H_2 , that is the positive and negative alleles at these loci were probably not in equal proportions in the parental varieties.

The ratio, $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$, that is, the ratio of the total number of dominant to recessive genes in all parents, was 0.97 (K_d/K_r in Table 11), which was close to unity, implying proximity between the numbers of dominant and recessive alleles in the parents.

The ratio h^2/H_2 (K) might be used to estimate the number of gene groups which control the character and exhibit dominance to some degree. Table 11 showed this value was equal to 2.46. So it could be inferred that there were at least three gene groups controlling ear length having some degree of dominance in this diallel.

In experiment (2) the t^2 -test for heterogeneity of W_r-V_r showed (Table 9) that Hayman's assumptions (1954b) were satisfied for all the eight diallels in this investigation. The P values were non-significant for all the diallels. From the standpoint of conformity to the model employed here, it therefore appeared that the analyses of the character were valid.

Table 9 a showed the mean square values for the sources of variance in the analysis of variance for ear length in all the eight 7 x 7 diallels. Each diallel was extracted from the 8 x 8 diallel (VI) by excluding one array at a time whose common parent was indicated at the bottom of the prefix P. The error variance for each of these diallels was derived from analysis of variance of F_1 -trials of each 7 x 7 diallel

as shown in Table 9 b. The results of the analysis of variance of the 7 x 7 half-diallel tables were identical to the perfect 8 x 8 half-diallel VI. The components a , b_1 , b_2 and b_3 were all highly significant and in complete agreement with diallel VI (Table 8 a). Hayman's method permitted here also to draw the (V_r, W_r) graphs (Fig. 6, c to j) and to make estimations of the various genetic components (Table 9 c) for the ear length character.

The linear regression lines of W_r on V_r for the eight 7 x 7 half-diallels were shown in Fig. 6 (c to j) excluding respectively array parent 1, 8, 2, 4, 3, 5, 6 and 7. The regression line in Fig. 6 c-A (Parent 1 excluded) is significantly different from unit slope ($P \approx 0.05$). The position of array 8, its common parent being the extreme recessive one, had been disturbed, showing a change in its order of dominance. In spite of this, the other array points, especially the dominant showed their normal relative order along the regression line. Although the regression line of unit slope through $\bar{W}_r$, $\bar{V}_r$ indicated overdominance, the actual regression line had rather shown a reduction in average degree of dominance over all arrays. The same trend was indicated in Fig. 6 g for the diallel with common parent number 3 excluded. This was the next dominant parent after number 1 in the group of parents. Here too the regression coefficient indicated a lower value, but was just not significantly different from unity. The order of dominance also was almost normal. The standardized deviation of y_r and $(W_r + V_r)$ was given graphically in Fig. 6 c-B for the diallel with array parent 1 excluded. The shift of array 8 from total recessiveness to an excess of recessiveness was also reflected here. But it was also revealed that this change of array 8 to less recessiveness had not been accompanied by apparent increase in ear length. Moreover, an evident linearity was maintained with a highly significant negative correlation, $r = -0.8864^{**}$.

The remaining six diallels, with one parent excluded, showed from their graphical analyses (Fig. 6 d-f, 6 h-j) remarkably consistent results in full agreement with that of the normal 8 x 8 half-diallel, from which they were extracted.

The estimates of the various genetic components and related statistics for the eight 7 x 7 half-diallels are given in Table 9 c.

The mean degree of dominance was denoted by $(H_1/D)^{1/2}$. These values for P_1 , P_3 and P_8 (diallels excluding array 1, 3 and 8 respectively) were 1.34, 1.07 and 1.09 respectively. These indications of overdominance in P_1 and a slight tendency of overdominance or rather complete dominance in P_3 and P_8 were also reflected by the graphical analyses in Fig. 6 c, 6 g and 6 d respectively. The $(H_1/D)^{1/2}$ values for the remaining diallels were all very close to unity (Table 9 c) implying almost complete dominance such as was indicated in the 8 x 8 half-diallel (VI).

The ratio of positive to negative alleles at loci exhibiting dominance, $H_2/4H_1$ was more or less of uniform values (varying from 0.22 to 0.25) for all the eight diallels, mostly closer to 0.25. This indicated that the positive and negative alleles at these loci were almost present in equal proportions in the parental varieties. The values of H_1 and H_2 ($H_1 \sim H_2$) would lead to a similar conclusion.

The ratio (K_d/K_r) of the total numbers of dominant to recessive genes in all the parents showed proximity to unity in general. However, in the two cases, where the most dominant or the most recessive parent was excluded, the diallels showed obvious decrease (0.75) or increase (1.47) of this ratio (Table 9 c). Exclusion of array 6 made the proportion equal, while in the remaining five cases the proportion of recessive genes was (in fact) slightly higher than for the dominant genes. This was in agreement with expectations.

The ratio h^2/H_2 , determining the number of gene groups which controlled the character, revealed values that varied from 2.0 to 2.8 for the different diallels. This could lead to infer that here there were at least three gene groups that controlled ear length, all three having about the same degree of dominance.

The mean degree of dominance as determined by $(AB/OB)^{1/2}$

and $(A^1B/OB)^{1/2}$ from the regression analysis (Fig. 6 c-j) also showed values (Table 9 c) closely resembling respective values estimated by $(H_1/D)^{1/2}$. The diallel excluding array 1, however, showed a $(H_1/D)^{1/2}$ value that differed from the $(A^1B/OB)^{1/2}$ value quite appreciably.

Experiment (4) was conducted with parents belonging to two categories of linkage condition. The first, diallel (VII), included parents (1, 2, 16 and 19) with two pairs of ert-mutant genes, ert-a²³ and ert-m⁴⁰, that were partially linked. The second, diallel (VIII), included parents 1, 17, 18 and 20 that involved two pairs of ert-mutant genes, ert-a¹³ and ert-d¹⁵ which were closely linked together. Each diallel was replicated twice in randomized block with F_2 family size that ranged from 102 to 161 individual plants in each plot. Parental family size was confined to 20 plants in each plot. As the block difference for each diallel was found almost nil (Table 10 b), the mean values for ear length were averaged over two blocks for subsequent analysis of each diallel table. Thus, the results were based on plot values for an appreciably increased number of segregating F_2 family plants. In the data on ear length, an average of two replicates was given for the arrays of a 4-parent half-diallel (Table 4 b).

The analysis of variance of W_r-V_r showed homogeneity over arrays for both the diallels VII and VIII (Table 10 c). This indicated that all assumptions of the analysis were fulfilled. In this experiment, however, linkage was shown by the genes introduced with the parents. Therefore, this test did not reflect the independent distribution of genes among the parents. Nor would the alternative test (ii) of Hayman (1954b) reveal any heterogeneity of W_r-V_r values for either diallel VII ($t = 2.04$; $P > 0.1$) or diallel VIII ($t = 0.2355$; $P > 0.8$). In a third test, the (V_r, W_r) regression coefficient was expected to be significantly different from unity if the assumption of no linkage was true. The results of this test (Table 11) did not indicate failure of any assumptions. The experimental data, therefore, seemed to have remained unaffected by the linkage situation.

Results from an analysis of variance are given in Table 10 a. In both diallel VII and VIII the component (a) was highly significant which indicated genetical variation amongst the parental varieties. The significance of (b_1) in diallel VII showed that the dominance was largely unidirectional. Component (b_2) in the analysis of variance was not significant; thus symmetry of gene frequencies having significant dominance was indicated (component b_2 is also zero when no dominance exists). Residual dominance effects were also shown to be absent by non-significance of (b_3).

In diallel VIII the component (b_1) was not significant, which could mean unbalanced dominance contributions to all crosses, that is, amongst the parents mean dominance had no unidirectional effects. Significance of (b_2), therefore, indicated asymmetry in the gene distribution amongst the parents. Here residual dominance effects were also shown by (b_3) becoming significant.

Analysis of the data in diallel VII gave a (Fig. 7 A) significant regression value $b = 1.1122 \pm 0.0565$ ($P < 0.01$) which was not significantly different from unit slope ($P > 0.1$). The regression line was nearer to the tangent point on the limiting parabola, indicating a reduced degree of average dominance in the arrays. The array number 16 had increased in proportions of dominant genes. This shift of parent array (number) 16 from recessive to dominant gene excesses (Fig. 7 A) had not been accompanied by substantial increase in ear length (Fig. 7 B). Fig. 7 B is a graphical treatment of the data on standardized deviations. Though a high numerical negative value for correlation coefficient was indicated between the variables, yet it was not significant ($P > 0.2$). This suggested a tendency (not significant) of recessiveness to be associated with dense ear and dominance to be associated with lax ear. In the regression analysis, the curved line of points (Fig. 7 A) through the intersection of $\bar{W}_r$, $\bar{V}_r$, suggested a correlated gene distribution, with genes of like effect associated in the same parent.

Diallel VIII gave (Fig. 8 A) also a significant regression value $b = 0.9212 \pm 0.1788$ ($P \approx 0.05$) and did not differ significantly from unity ($P > 0.6$). The regression line was very near to the limiting parabola, indicating a small degree of average dominance over all arrays. The order of the four parents show a relative position along the regression line in accordance with their "ear length" characteristics. A clear curvature, concave downwards, of the distributed points suggested a correlated gene distribution with genes of like effect associated in the same parent. For V_r , W_r , V_p and $(W_r + V_r)$ of the two diallels, see Table 12.

In Fig. 8 B the standardized deviations are shown. The correlation in the distribution of co-ordinate points was less obvious, having numerically a high coefficient value but still fell just short of becoming significant ($P > 0.1$). This loss of significance might reasonably be a result of the small number of parents. Thus, relation between dominance and recessiveness on the one hand, and lax and dense type on the other has become less suggestive.

Estimation of genetic components:

The various genetic components and other statistics estimated from the mean values of parental varieties and their progenies are given in Table 11.

$(H_1/D)^{1/2}$ for diallel VII, an overall measure of the degree of dominance, was equal to 0.28 which indicated partial dominance (much reduced) in the F_2 . The apparent degree of dominance would typically be less than that found in the F_1 , as the contribution of H , the variation contributed by the heterozygote, was halved in the F_2 , as compared to the F_1 (Mather, 1949). When estimated by $(AB/OB)^{1/2}$ from regression analysis, the value was 0.33. The ratio of positive to negative alleles at loci exhibiting dominance, $H_2/4H_1 = 0.17$, indicating an asymmetrical proportion of positive to negative alleles at loci exhibiting dominance. The ratio, $K_d/K_r = 1.98$, represented the proportion of dominant to recessive genes in all parents.

$h^2/H_2 \left[\frac{(\bar{P} - \bar{F}_1)^2}{1/4 H_2} \right] = 2.07$ estimated the number of gene groups which control the character and exhibit dominance to some degree. So it might be inferred that there were at least two gene groups controlling ear length in this case, having some degree of dominance.

In diallel VIII, the mean degree of dominance as given by the ratio $(H_1/D)^{1/2} = 0.44$ indicated partial dominance. Conversion to equivalent values for F_1 (0.88) showed quite strong partial dominance. The mean degree of dominance estimated by $(AB/OB)^{1/2}$ from regression analysis was 0.43 which agreed closely to the value determined by $(H_1/D)^{1/2}$.

The ratio of positive to negative alleles at loci exhibiting dominance, $H_2/4H_1 = 0.19$, indicated considerable asymmetry.

The ratio K_d/K_r , that is, the ratio of the total numbers of dominant to recessive genes in all parents, was 1.38. These values are affected by gene interaction and can be higher than would be expected in a diallel showing no interaction.

The ratio, $\frac{(\bar{P} - \bar{F}_1)^2}{1/4 H_2} = 1.90$, gave the estimation of the number of gene groups which control the character and exhibit dominance to some degree. It showed that at least two gene groups were present in this diallel controlling the character that exhibited some degree of dominance.

Discussion

Choice of parental lines in these experiments was based on the need of previous knowledge of genic background to determine whether more or less precise results are produced as indicated and determined in the theory of diallel analysis following Hayman (1954a, b). In the breeding of self-pollinating crop plants a breeder depends on lines derived from a highly selected population. The effect of such selection upon the results of diallel analysis, as compared to results obtained from random samples of inbred lines derived without selection from a randomly mating population at genetic equilibrium, is not known. The reason for this is that no suitable data are available to which the method discussed can be tested. The model used in the present investigation accounts for the diallel theory with the experimental materials reflecting the situation in a more or less randomly mating population about which valid inferences can be made. Origin of parents has a definite bearing on Hayman's (1954a, b) six assumptions in the analysis of diallel crosses. The lines utilized here fulfilled Hayman's all assumptions as previous studies and observations had verified all of those conditions. Hayman's assumption 6, requiring independent distribution of genes between the parents, has received particular emphasis from Kempthorne (1956). Such criticism could not be made of the plant materials used in the present experiments. Jinks (1954, 1955) and Hayman (1954b) considered their methods as a test for Hayman's assumption of independent action of non-allelic genes, provided all other assumptions were fulfilled. Hayman (1954b) has also discussed the complexity of multiple allelism. The failure of these three assumptions, namely (a) selection of random samples, (b) no multiple alleles, and (c) uncorrelated gene distribution which have received so much attention because of their complexities has, therefore, been taken up as an important part of this investigation. It was because of the unique suitability of the material that experimental models could be set up to deliberately fail these assumptions in separate experiments.

Crumpacker and Allard (1962) reported on an investigation to determine the usefulness of the Jinks-Hayman type of analysis in the breeding of self-pollinating crops. "Heading date" in wheat was used as the test character in a diallel cross among 10 varieties. The information they derived from the analysis evidently was successful in revealing the major features of the genetic system governing heading date in the 10 parents investigated and agreed closely with observed segregation in various generations of the seven critical hybrids. Since this diallel analysis did not provide precise information about the polygenic system, any predictions about the rate or extent of progress (expected from hybrids between any two parents) were

difficult. The diallel cross analysis provided in this case at least an assessment of the genetic system that appears to be useful in predicting the immediate effects of selection for heading date, but not the ultimate effects of an appropriate combination of intercrossing, inbreeding and selection. The diallel analysis was not successful in providing precise information about this identified polygenic system, probably because of the overwhelming and obscuring role of the major genes in setting the pattern of genetic variability.

Kearsey (1965) comparing five experimental designs of biometrical analysis, in a random mating population, for variation in flowering time in Papaver dubium, concluded that the half-diallel cross (Hayman, 1954a, b) gave the best information about the small number of plants used. Good agreement with the observed statistics was obtained and it is likely to be the most reliable of all the designs.

Leffel and Weiss (1958) conducted experiments to evaluate parent- F_1 hybrid relationships in soybeans for certain agronomic and chemical characters. It was the first of a series of experiments concerning early generation testing and recurrent selection in this material.

The split-plot analysis, the analysis of combining ability (model following Griffing, 1956), and the analysis of diallel crosses (following Jinks and Hayman, 1953) were similar in detecting lines exhibiting unexpected performance in the F_1 generation. The interpretations and significance of these crosses, deviating from the additive scheme, suffer from the same pitfalls as they did in other studies: the questionable role of interaction among allelic genes, interaction among non-allelic genes, and linkage. Non-allelic gene interaction as an interpretation of heterosis can be confirmed from subsequent generations but it would seem that the problem still remains the same as in the past. It is a common occurrence in investigations of quantitatively inherited characters that lines are not recovered in later generations as vigorous as the F_1 generation, and this fact is very often accepted as conclusive proof of over-dominance.

The two diallels III and IV showed a condition of gene asymmetry (b_2) in all of the parents. This was also a natural consequence of interaction of multiple alleles introduced into these alleles. Although diallel II also included multiple alleles, the effect due to their phenotypic difference in "ear length" was so minor and their interallelic interaction so ineffective, if any, that the total disturbing effect on the diallel analysis was

negligible. As expected, the graphical analysis for the same experiments also depicts the interallelic interaction effect on the graph by their movements to the right and an increase in the dominant effect. It is important to observe here that linkage and gene interaction can resemble one another in their effects.

Forty five diallel crosses among 10 soybean parents were studied by Leffel and Hanson (1961) in the F_1 , F_2 spaced, F_2 bulk, F_3 bulk, and F_3 line generations. (The basic plant materials for these studies were described previously by Leffel and Weiss (1958).) Data for these generations were subjected to different analyses to determine the average and specific contributions of parents to progenies with regard to epistasis, dominance, and additive gene action. Average contributions of parents were especially prominent for seed yield and size and for plant maturity. Specific effects of parents for plant maturity and plant height were identifiable by the combining ability method proposed by Rojas and Sprague (1952) but not by the regression of array covariances on array variances as proposed by Jinks and Hayman (1953). Performance of parents or their crosses in early bulk generations were reliable predictors of the performance of lines obtained from the crosses in the F_3 line generation.

In general, the data indicated the parental prepotency or ability to produce a certain effect in the F_n progeny for all characters, prominently for seed yield, plant maturity, and seed size. The associations between all generations studied suggest the possibility that all generations, with the possible exception of the F_1 , are of value in predicting the value of crosses when tested adequately in time and space. It was impossible to evaluate the role of genotype-environment interactions in the F_1 generation of this study as this generation was tested in only one environment. Performance of soybean parents was as reliable in predicting the value of crosses as was the performance of bulk populations of crosses; however results of these experiments indicate that testing of bulk populations will be of value in identifying crosses yielding the most desirable segregates.

Gilbert (1958) considers such a "polygene" analysis being of no direct use to the practical breeder unless it causes him in some way to alter his breeding programme for the better. As these genes are individually unrecognizable, the analysis has to be concerned with their combined action as revealed by the various statistics. He insists that the concepts of dominance, epistacy and so on are more complex in polygene analysis than in Mendelian genetics.

In polygene analysis, for example, the possibility of lethality is ignored, and dominance is taken to mean any departure of the effect of Aa from the average of the effects of AA and aa. He also considers the change of scale. First, it produces such consequences that the genetic labels such as dominance or complementarity are easily confused in the results obtained in practice (Hayman, 1954b). Secondly, alternative genetic systems characterized by, e.g., purely multiplicative gene effects could be analysed in the polygene way in terms of additive gene effects and their various types of interaction, i.e. dominance, epistacy, etc. The idea of additive independent gene effects - treating departures from this simple scheme as genic interaction - is employed solely because it leads to simplicity in the statistical analysis. He also thinks the deleting of data to fit the hypothesis is highly debatable. The results of such a selective analysis cannot be supposed to have any wider inductive application except to materials that have been similarly selected. The same objection applies to Hayman's alternative recommendation that a particular progeny may be disallowed, and the missing-plot technique used to replace it. It should not be used to replace egregious and unwelcome (but perfectly genuine) observations. He also objects to the way in which the data are made to fit the hypothesis. By making an eighth assumption, of equality and absence of oppositions in the dominance effects of the various genes, Gilbert suggests that it is possible to estimate the number of loci involved.

Kempthorne (1956) points out that the assumption of genes being independently distributed between the parents, remains crucial, and he insists that the parents must be the result of unselected inbreeding from a random mating population. Gilbert thinks that Kempthorne's claim at least gives some justification to this assumption. Thus, Gilbert (1958) concludes that "the polygene analysis of a diallel cross suffers from several theoretical defects, but in any case its results do not appear to be directly relevant to practical breeding work. The performance of the parental varieties themselves gives valuable prediction of the relative behaviour of the crosses, but the diallel cross does give further information. Whether it might be used for assessing long-term potentialities of raw material at the beginning of a long breeding programme is unknown."

Gilbert has given a critical evaluation of the diallel-cross technique. His criticism of the basic genetic assumptions of the technique is not only categorical but also invokes eventualities, near and remote. It implies that the statistics involved must be inferentially valid. His conclusion that the value of this technique is exaggerated and that information gained from it, is little more than that obtainable from the parents themselves is well taken on many points. But yet it seems that he fails to quite appreciate that a

statistical-genetic analysis must be based upon statistical assumptions and produce a statistical result. This along with the consideration that a poly-genic system is involved, makes it rather unfair to expect that the diallel analysis will give results anything like those obtainable from classical Mendelian analysis. He also fails to justify, genetically at least, his insistence on valid statistical inference. The fact that a method of analysis is statistical does not necessarily establish statistical inference binding with the genetic conclusion. It should be viewed as only seeing it less directly. This system at least has two main advantages: experimentally, a systematic approach; and analytically, an over-all genetic evaluation useful in identifying, in an early generation, crosses of best selection potential.

In choosing parents, one would always be tempted to disregard the rule that they be taken at random. It involves the question of inferential validity, and perhaps a relation to random mating, but our consideration of this would always be less important than our interest to practical knowledge of parental material at hand. It seems from the present experiments that such anxiety on inferential validity is unfounded in the context of practical beneficial information gained (diallel VI c-j). Nearly all the results presented here, provide concrete basis against the reputation of Gilbert's statement that, for the plant breeder, the information gained from analysis of diallel crosses is little more than that obtained from the parents themselves. The diallel analysis in these experiments provided full information on the genetic identity of the character "ear length", on dominance-recessive relations, on genic interaction, and on linkage association. The information greatly outweighs that obtainable from parental observations and will, therefore, provide invaluable guidance in a plant breeding programme.

The diallel cross graphs (expts I, V, VI) were almost identical from block to block, indicating that genotypic-environmental interactions were quite negligible. This conclusion has supporting evidence obtained from statistical tests of various genetic parameters. These results, therefore, reflect the good correspondence between genotype and phenotype for the experimental materials. In some cases (expts II, VII and VIII) where failure of certain assumptions were deliberately introduced, appropriate tests failed or just failed to reveal a significant effect of this. The experimental data in such cases seemed to have remained more or less unaffected by an introduction of gross biases into the genetic analysis.

With a normal diallel cross it is possible to make necessary inferences quite effectively. The resulting information about the genetic system, therefore, can provide a basis for the prediction of patterns of segregation in specific crosses.

In the present experiments involving 4×4 diallels, it is of interest to note that when the assumptions are valid or at least if there is no epistasis involved and only two alleles per locus are assumed, then the components (b_2) and (b_3) have a clear explanation of results. This is because the genes which contribute to the variation belong to one of two cases. In the first case a situation can be so that one allele is present in one of the parents and the other allele in the remaining three parents, while in the second case one allele is present in two of the parents and the other allele in the other two parents. In both cases, if the genes are balanced so that their dominance-contribution to all crosses are the same, they affect only (b_1). When the genes are not balanced, in the first case they contribute to (b_2) and not (b_3), but in the second case the genes contribute to (b_3) and not (b_2). The perfect diallel V reveals precisely the same effect. Diallel I deviates by showing (b_2) significant at the 5% level.

If all the genes with dominance effects belong to the second case, then the condition of independent gene distributions is satisfied. Hence if (b_2) is not significant, any apparent departure of the V_r , W_r graph from a straight line of unit slope is certainly not significant. The opposite may not be usually so, but (b_2) can ascribe a fuller meaning to the "upsets" in the V_r , W_r graph for the 4×4 diallel.

The information provided by experiment (2) not only applies to the population as constituted by the parents of the diallel cross but may also apply to a more or less randomly selected sample from a large population involving the same genotypes. With the exception of array 1 (with all dominant alleles in the common parent) the exclusion of all other arrays, one at a time from the 8×8 half-diallel (VI) has given results that are in good agreement with the normal diallel. Striking similarity existed in the average degree of dominance. Order of dominance showed a remarkable resemblance, specially of parents with an excess of dominant alleles. Parent 6 (with an excess of recessive alleles) expressed quite evidently increasing dominance in absence of a parent which was more dominant. In general, parent 5, 6 and 7 had their mutual change of position along the ascent of regression line and also in their order of dominance (measured from $W_r + V_r$ values). Small shift of position within these parents could be considered of minor significance if it was borne in mind that these three parents with an excess of recessive alleles had formed a close group along the regression line in the normal (perfect) 8×8 half-diallel. Consequently it is apparent that (unless an extreme dominant parent is excluded) a non-random selection of parent

materials has no adverse effect on the expected results. This consistency of results with predictions indicate the usefulness of the method.

A theoretical investigation of the effect of multiple allelism on the diallel analysis procedure has been carried out by Oakes (1967). He concluded that, whenever combinations of loci occur at which, in the parental lines, there are only two genotypes out of the possible three ones then, irrespective of what those genotypes be, the V_r , W_r graph is always a straight line of unit slope. Hayman (1960a) showed that the measure of dominance is not seriously disturbed by multiple allelism.

When the regression line moves downwards to the right it denotes increasing dominance. An over-dominance is then indicated if the regression line and the W_r ordinate intercept below the origin. With interaction between the parental genes the slope of the regression line would give a significant deviation from unit slope ($b < 1$). In diallels III and IV which involve multiple alleles the regressions are less significant and the slopes are different from unity ($P \approx 0.1$ in both).

Diallel II involving allele a^{36} is slightly less in dominance as compared to diallel III which includes allele c^{97} . This increase in partial dominance turns almost to complete dominance when both alleles a^{36} and c^{97} are included in diallel IV. Moreover, the regression lines in both diallels III and IV move markedly downwards showing a clear departure from unit slope. This denotes an interaction between parental alleles. The regression lines, in fact, intercept the W_r ordinate below the origin, and this shows clearly a tendency towards over-dominance.

It is also obvious that allele a^{36} , which differs insignificantly in "ear length" character from that of allele a^{23} , neither appreciably changes in allelic expression, nor interacts with its allele in the parents. On the other hand, when it differs considerably in character expression with c^{97} , it produces interaction and comparatively less recessive effect, as is evident in diallel IV.

Although the correlation coefficients in these two diallels (III and IV) fail to reach significance, yet the parental genotypes and their relative positions on the regression line are quite evident. That no significant correlation is found between y_r , the mean of the common parent, and $(W_r + V_r)$, is indicative of the fact that dominance is not unidirectional. It is, however, more likely that in these cases non-significance of the correlation coefficients for the coordinate points, in spite of their numerically high values

(-0.8961 and -0.9388, respectively, in diallels III and IV) is a consequence of the small number of parents involved.

The general picture emerging from the present analysis is that an increasing involvement of multiple alleles at different loci affects the overall dominance level, but as regards the order of dominance the change is very small. In the light of the correlation values obtained for $(W_r + V_r)$ and y_r for "ear length", the dominance relationship is obvious. Diallel analysis may in such cases, no doubt, forward information about quantitative genetic control of certain characters.

From results it is apparent that the main effects of correlated gene distributions are clearly recognizable and, moreover, that association can be distinguished by giving a characteristic pattern, i.e. an upward curvature of the regression line in the V_r, W_r graph. Hill (1964) has reported similar results in his investigations on correlated gene distribution in the analysis of diallel crosses. He described experiments with inbred lines of Drosophila melanogaster which were designed to simulate the effects of the two types of correlated gene distributions - association and dispersion. He provided information also to distinguish association from dispersion. Associated distributions produced a significant upward curvature on the V_r, W_r graph as detected both by the graph itself and subsequent multiple regression analysis. Dispersion, on the other hand, did not give any distinctive curvature to the graph. In general, correlated gene distributions appeared to have little effect on the estimates of the relative proportions of dominant and recessive genes which each parent contains, although difficulties might arise when estimating this in the presence of dispersion. Non-random gene distribution does, however, alter the apparent level of dominance, association resulting in an underestimation, and dispersion, in an overestimation.

The present investigation also revealed the same characteristic when concerned with association (Fig. 7 and 8). It was clearly noted that such non-random distribution of genes had little effect on the order of array points along the graph. Moreover, such a distribution did affect the apparent level of dominance, giving an underestimation.

It rather becomes a matter of concern to discriminate between the effects of non-random gene distributions and those of gene interaction. It is because the two mimic one another to a certain extent in the nature of the disturbance which each can create on the V_r, W_r graph. A superficial resemblance is quite striking between effects of duplicate type of interaction and association,

both being conspicuous with a curvature concave downwards. Dispersion again has a pronounced similarity with complementary type of interaction whereby curvatures concave upwards arise in both cases. Generally, curves stemming from duplicate interaction would not be expected to depart so much from the straight line compared to such stemming from complementary interaction. Curves concave downwards remain shallower than curves concave upwards. But, in the main, reverse is the case with correlated gene distribution (Mather and Jinks, 1971).

There can be a profound difference in the effects of association and dispersion, depending on the number of loci involved. Both association and dispersion is possible when there are two pairs of genes, the effect being equal and opposite. When there are several pairs of genes, all of them can be in association relative to one another, but not in dispersion. This is just as with linkage where "any number of genes can be coupled but not all of them can be in repulsion with one another if more than two loci are involved. Thus with more than two loci a mutually reinforcing system of departures from rectilinearity of the W_r/V_r relation can arise from association, but not from dispersion. The maximum curvature which is concave downwards is then greater than the maximum curvature which is concave upwards." (Mather and Jinks, 1971).

Since the results of a set of diallel crosses are based on family means or, more specifically, means of true breeding lines and their F_1 s, linkage as such has no effect on it. But it may be affected by a phenomenon somewhat similar to linkage, and one that at times is a consequence of gene linkage. This phenomenon is the departure from independence of the genes in their distribution among the parental lines.

For the linkage experiments (diallels VII and VIII) it is remarkable that none of the tests had been able to reveal the actual genic situation, i.e. failing of the assumption of non-random distribution of genes in the parents. Both the tests for heterogeneity of $W_r - V_r$ were insignificant implying an independent distribution of genes among the parents. The third test also, contrary to expectation, failed to show V_r , W_r regression significantly different from unit slope. The cause may be that the total change in the diallels owing to linkage was too small to produce severe upsets in the results. This is especially true for diallel VII (Table 10a), having a weak linkage. High significance of component (a) in both diallels was corroborated by pronounced genetic variation amongst the parental varieties. While diallel VII showed unidirectional dominance, there was an unbalanced dominance contribution to all crosses in diallel VIII. Again, symmetry of gene frequencies having

significant dominance, was indicated in the case of weak linkage (diallel VII). In contrast an asymmetry in the gene distribution was expressed in the strong-linkage situation (diallel VIII). The latter included a residual dominance effect while such an effect was not identified in the former (diallel VII).

A very small degree of average dominance over all arrays was conspicuous in both the diallels. This was shown by their regression lines lying close to the limiting parabola (Fig. 7 and 8). Genetic background of the parents was not equally informative in both the diallels. While both showed significant regression values and order of parental dominance with agreeable relative position along the regression line, the tendency of recessiveness to be associated with dense ear and of dominance, with lax ear, was more suggestive in the former (diallel VII) than in the latter (diallel VIII). Insignificance of the correlation coefficients, in spite of their high numerical values ($r = -0.7181$ and -0.8537 in diallels VII and VIII, respectively) might be a result of the small number of parents (only 4). The various estimated genetic components delivered an (acceptable) information about the actual genetic situation in the parents. The much reduced partial dominance was mainly due to the contribution of H (the variation contributed by the heterozygote) being halved in the F_2 , as compared to the F_1 .

Summary

The theory and potentialities of the method of diallel analysis (according to Hayman and Jinks) has been investigated. As a model material different "ert-mutants", affecting the character "ear length" in barley, were utilized. The following four conditions were considered:

(a) Diallels with all possible parents constituting the theoretical population, were set up. They involved two or three ert-mutant genes. This constituted perfect diallels that satisfied all basic assumptions of the diallel theory. The results showed a good agreement with the genic information and theoretical expectations for the parents.

(b) In order to study the effect of a non-random selection of parents, one parent at a time was excluded in the analysis of the above 8 x 8 diallel. The results were in most cases in accordance with the perfect diallel.

(c) The effect of multiple alleles was studied using four sets of (4 x 4) full diallel crosses (one of these was a perfect diallel cross serving as a control). There were some effects which increased with involvement of multiple alleles in an increasing number of loci. Considerable information could yet be derived from such a diallel analysis.

(d) The effect of linkage in F_2 population was studied using two 4 x 4 diallels which included two ert-mutants each, partially or closely linked respectively. Analysis gave a characteristic curvature (concave upwards) of the regression line. It was more prominent with a strong linkage.

As revealed by these experiments, the diallel analysis can be profitably employed as an integral part of a basic quantitative genetics study.

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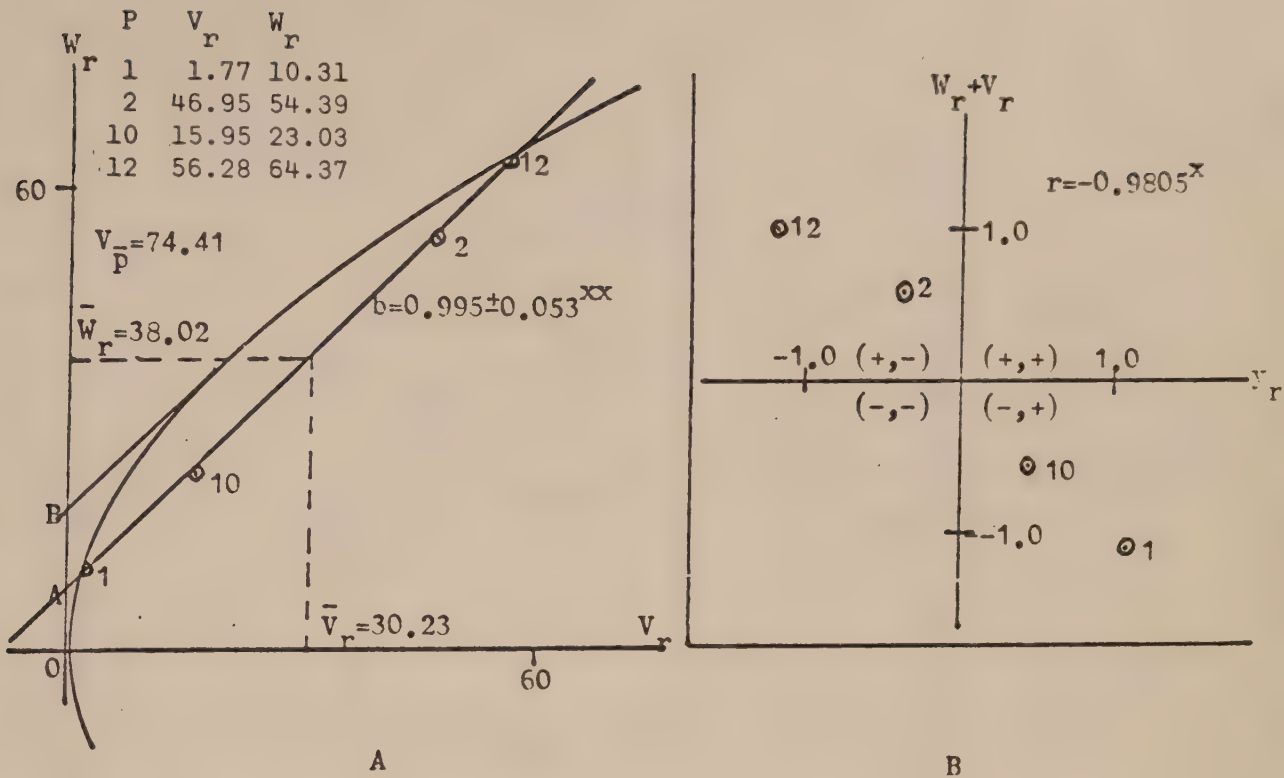


Fig. 1. F_1 . Diallel I.

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

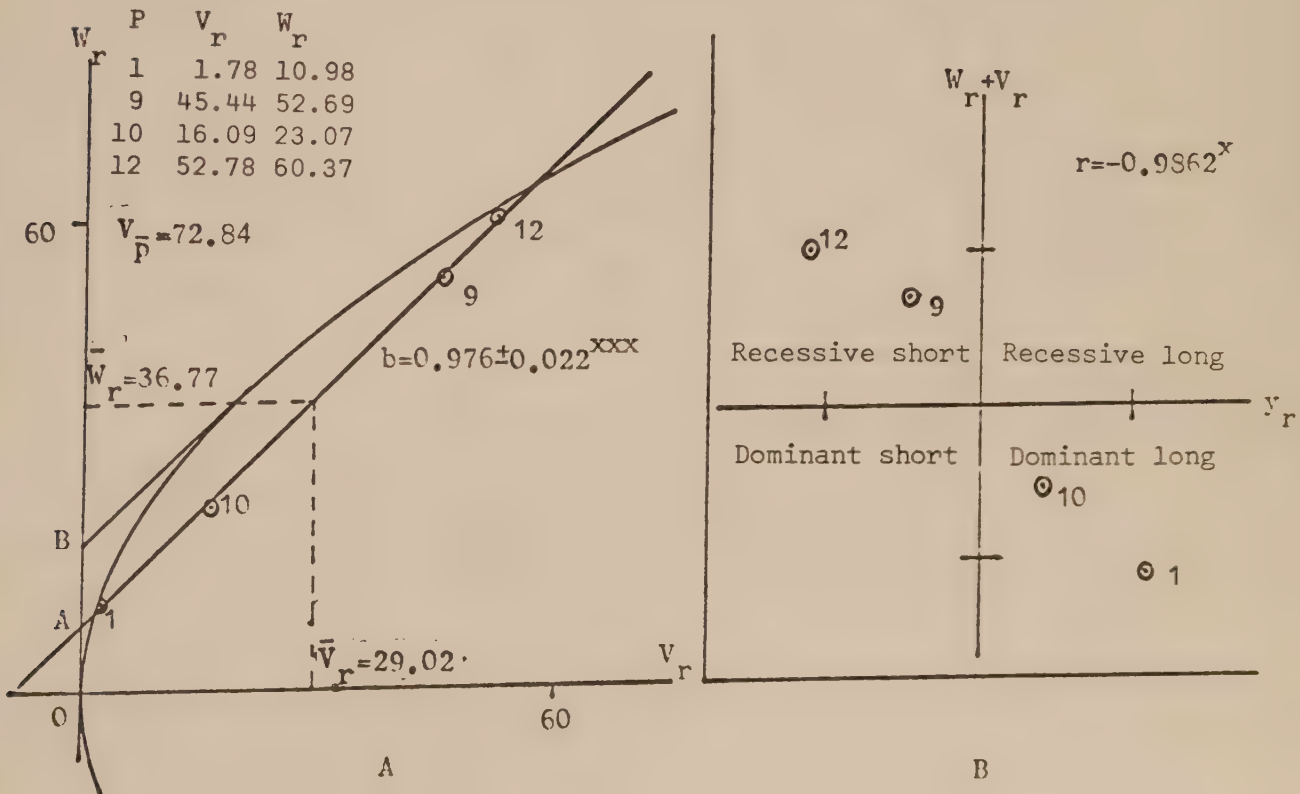


Fig. 2. F_1 . Diallel II.

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

x Significant at 5% level
 xx Significant at 1% level
 xxx Significant at 0.1% level

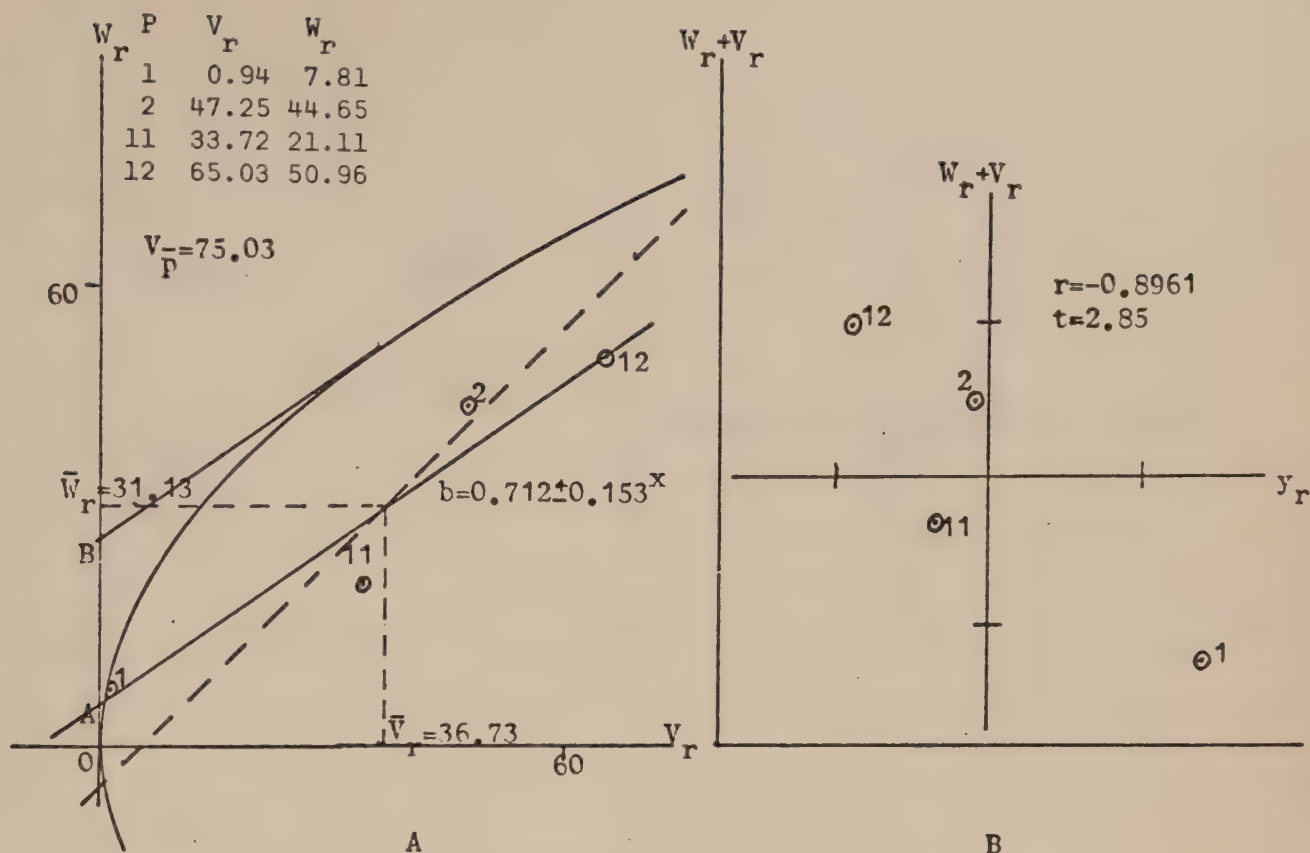


Fig. 3. F_1 . Diallel III.

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

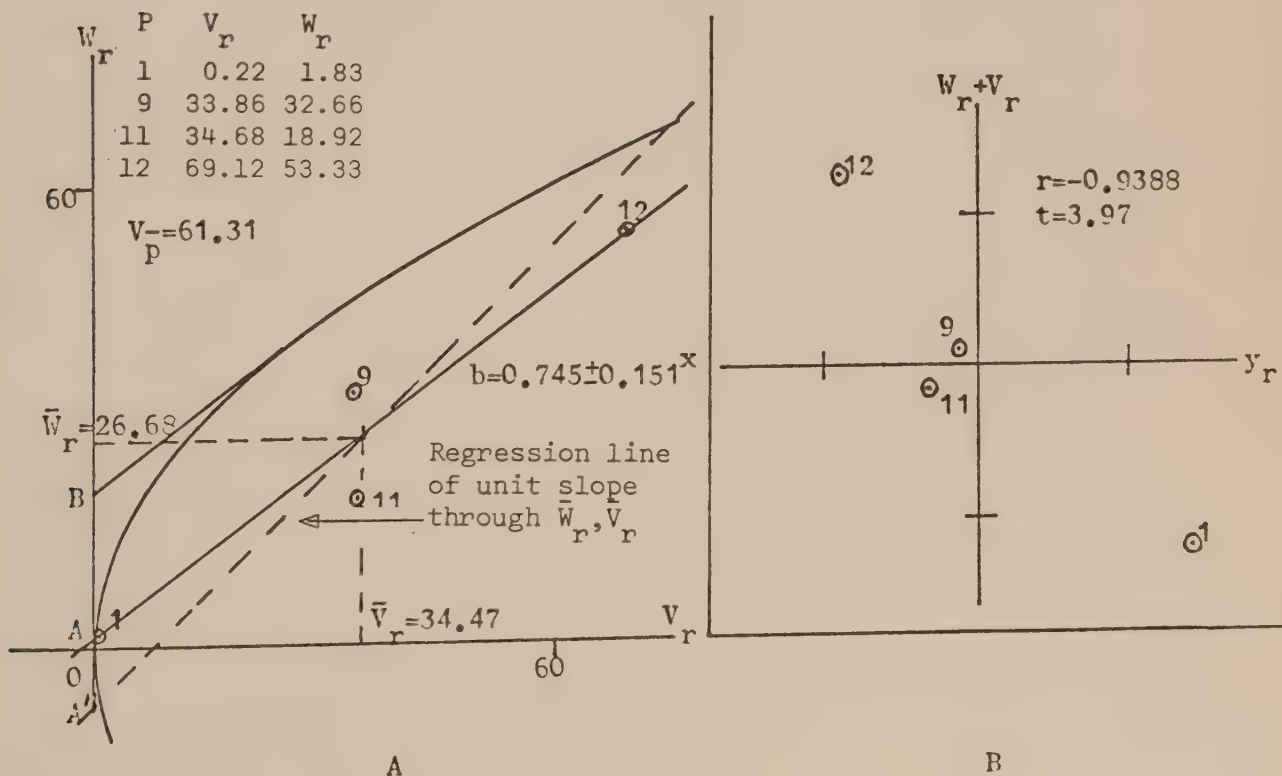


Fig. 4. F_1 . Diallel IV.

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

x Significant at 5% level
 xx Significant at 1% level
 xxx Significant at 0.1% level

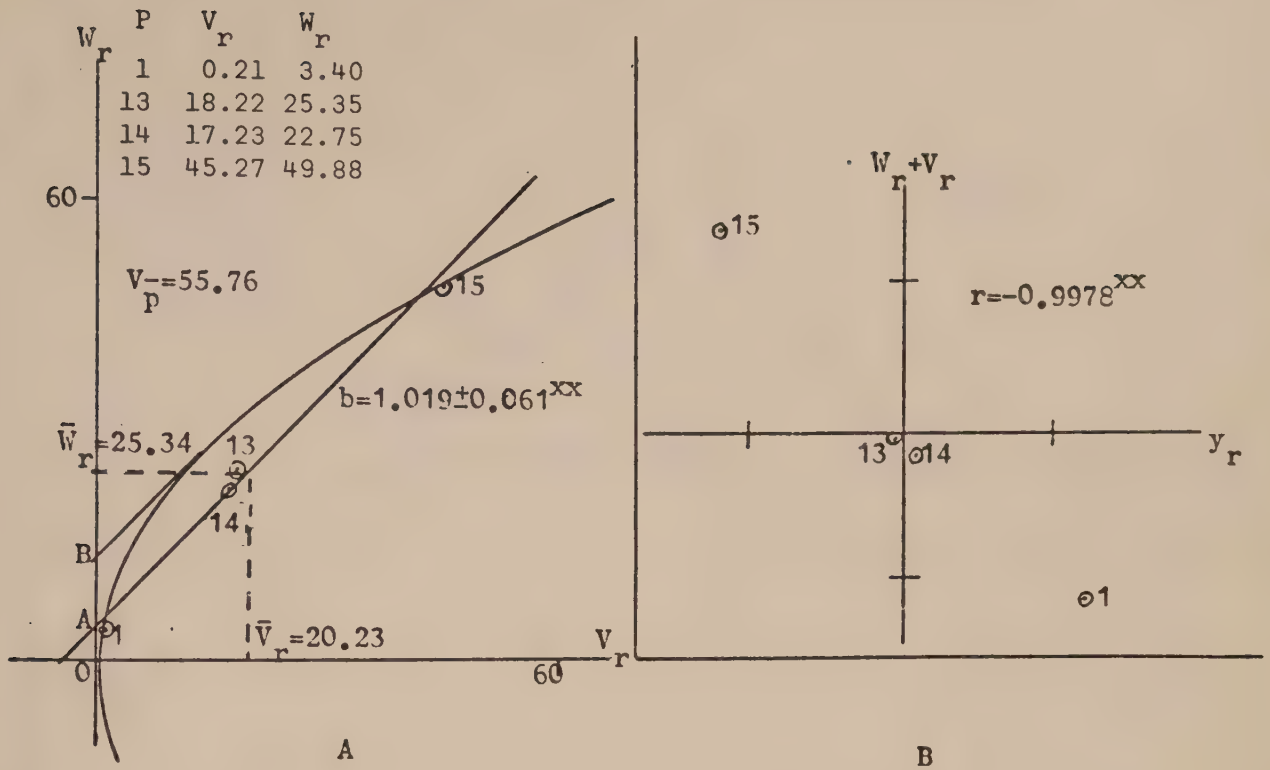


Fig. 5. F_1 . Diallel V.

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

x Significant at 5% level

xx Significant at 1% level

xxx Significant at 0.1% level

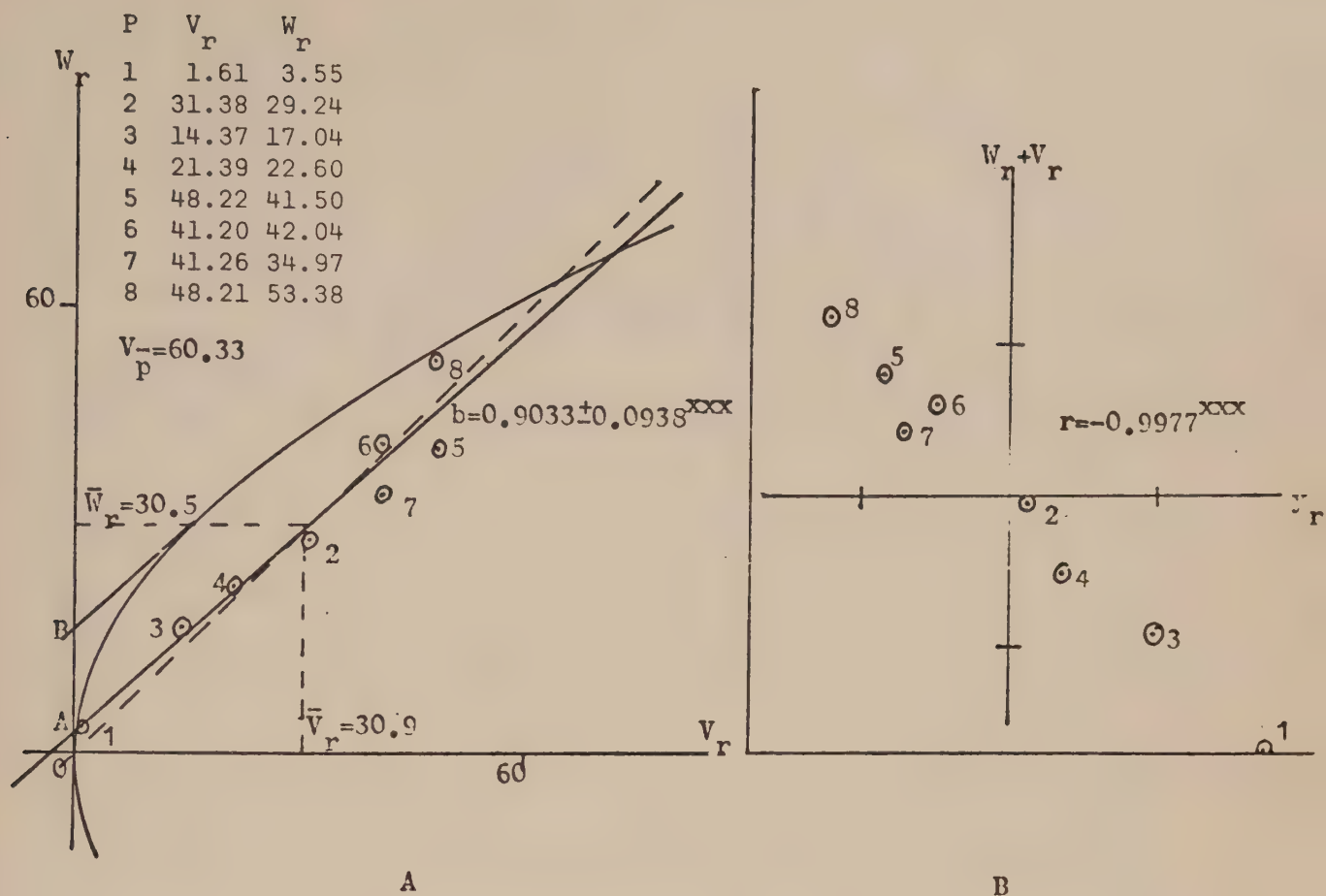


Fig. 6. F_1 . Diallel VI. (Pooled over two replications.)

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

x Significant at 5% level
 xx Significant at 1% level
 xxx Significant at 0.1% level

P	V_r	W_r
1	1.6	1.3
2	31.9	29.7
3	14.9	14.4
4	20.1	22.3
5	49.9	42.4
6	45.1	43.8
7	42.6	36.6
8	49.7	53.5

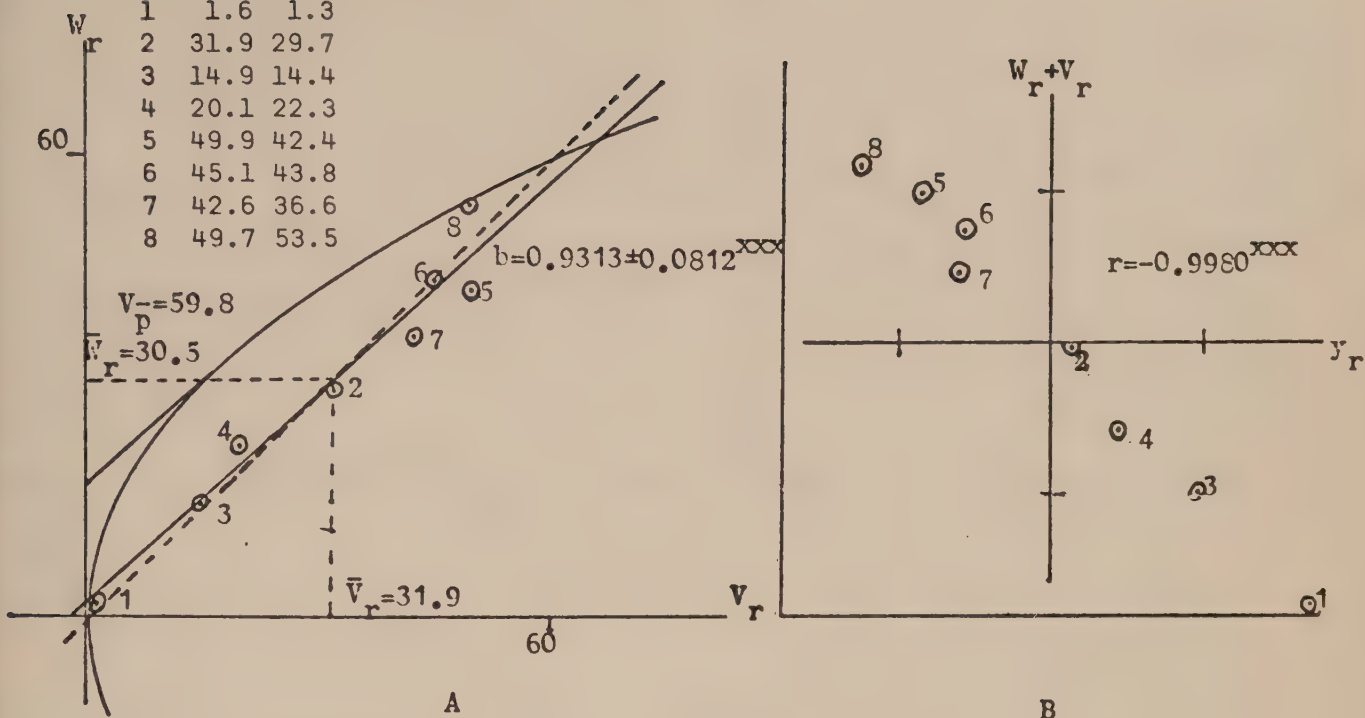


Fig. 6a. F_1 . Diallel VIa.

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

P	V_r	W_r
1	2.9	6.2
2	30.9	28.9
3	14.5	19.8
4	23.2	23.1
5	46.8	40.4
6	38.0	40.7
7	40.6	33.7
8	46.8	53.3

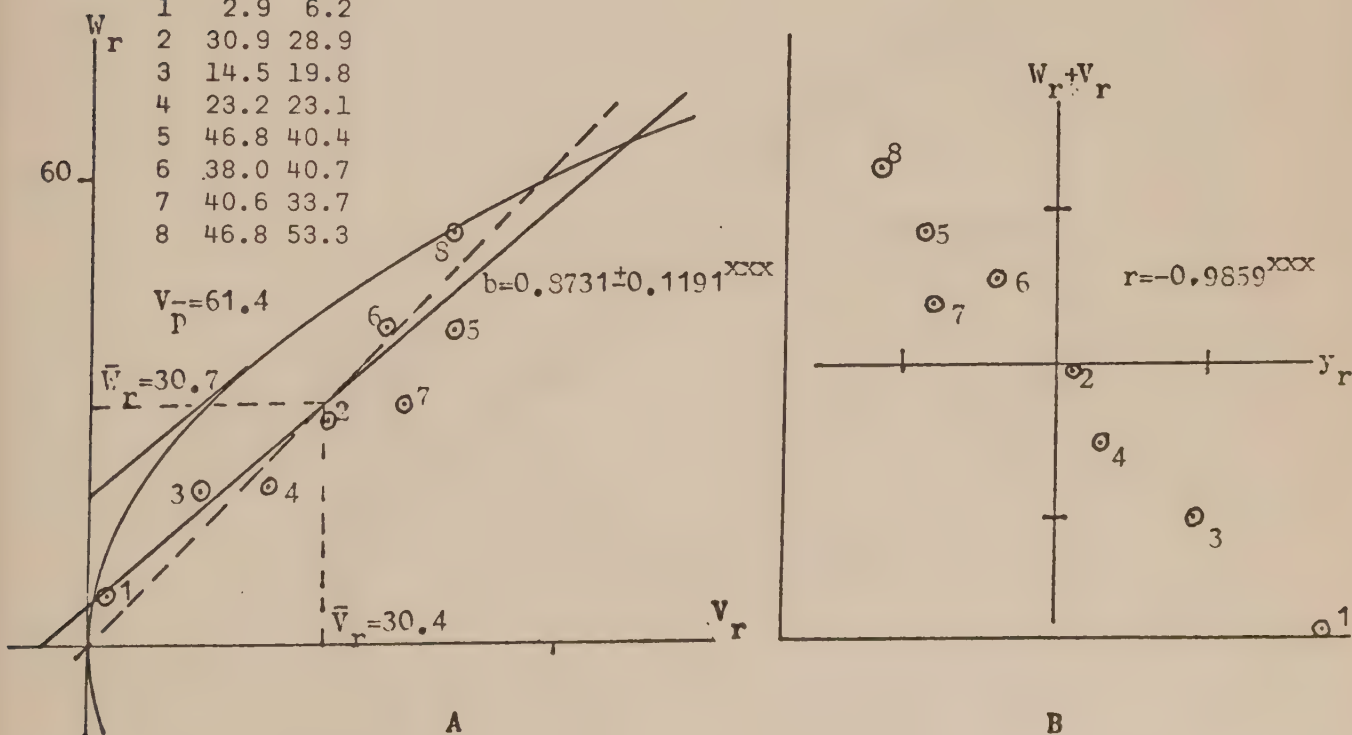


Fig. 6b. F_1 . Diallel VIb.

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

x Significant at 5% level
 xx Significant at 1% level
 xxx Significant at 0.1% level

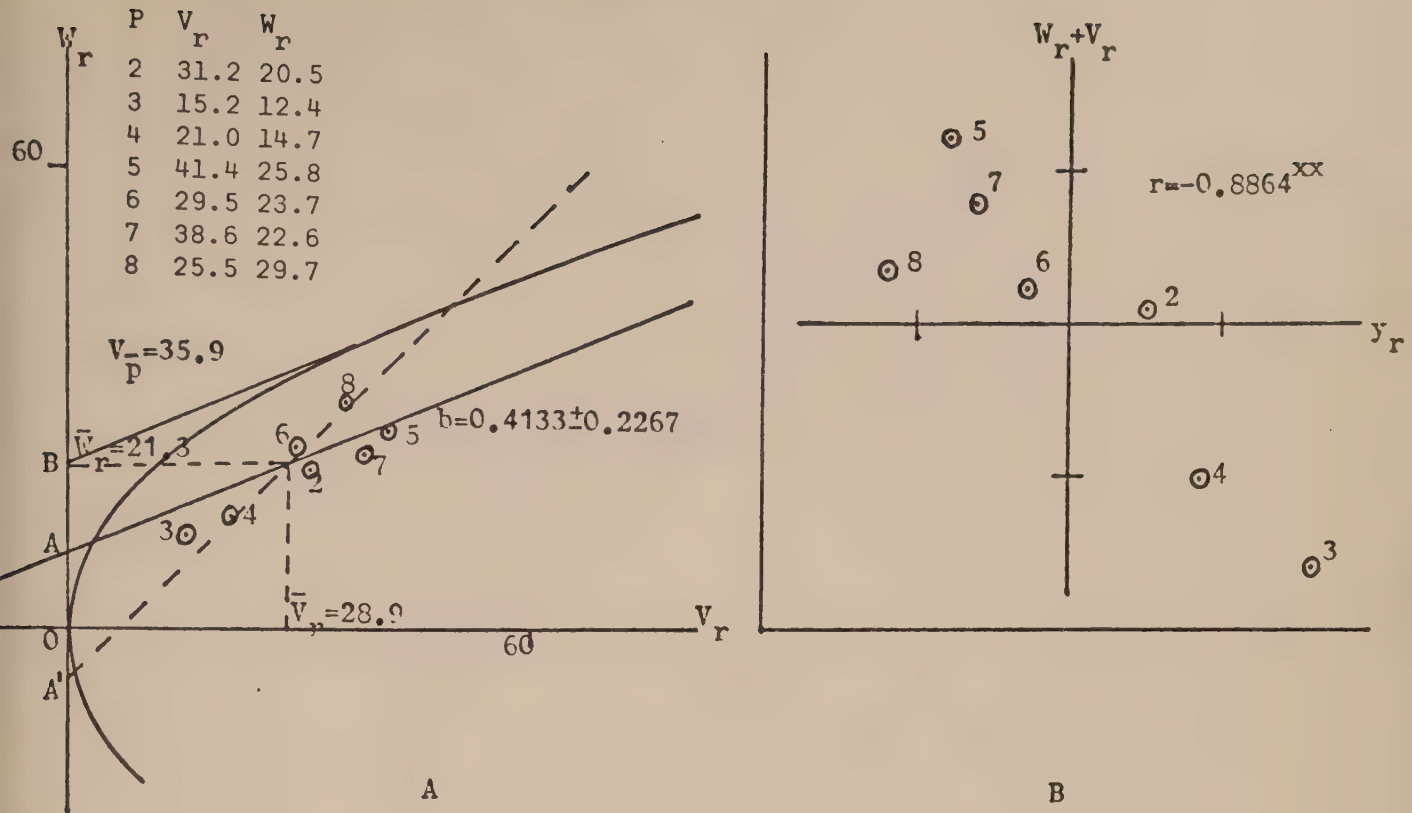


Fig. 6c. F_1 . Diallel VI- P_1 .

A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

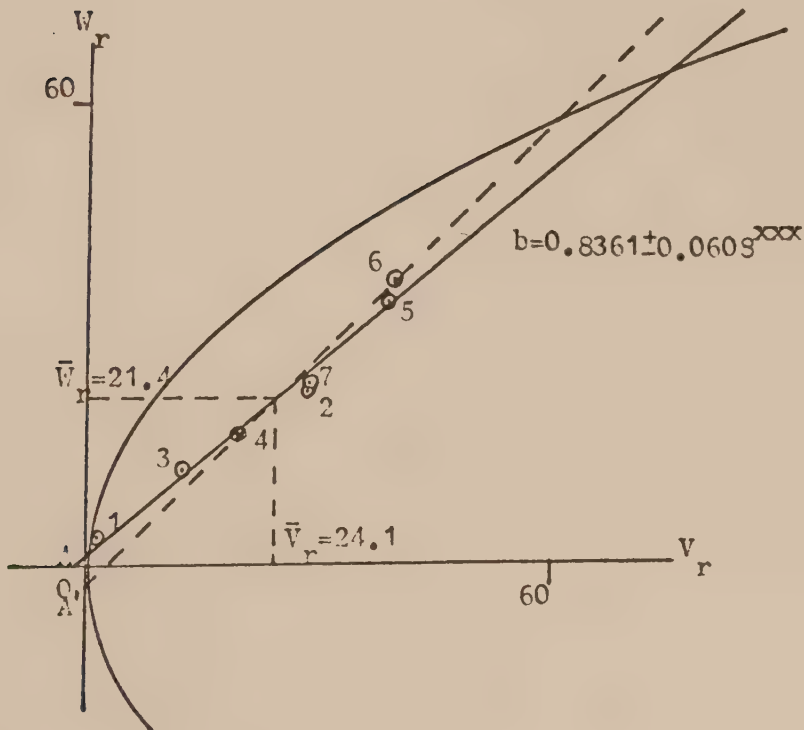


Fig. 6d. F_1 . Diallel VI- P_8 . V_r, W_r graph.

x Significant at 5% level
 xx Significant at 1% level
 xxx Significant at 0.1% level

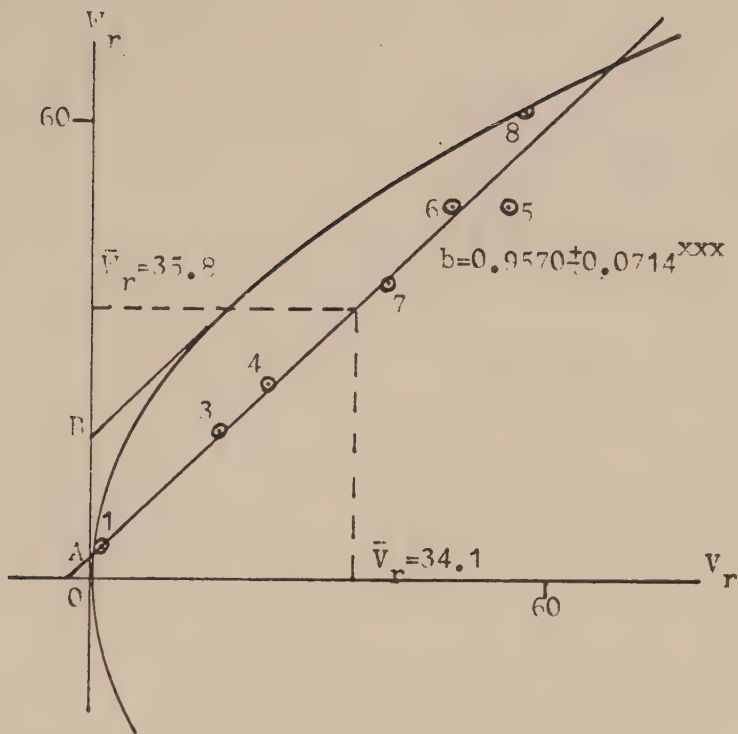


Fig. 6e. F_1 . Diallel VI-P₂. V_r, W_r graph.

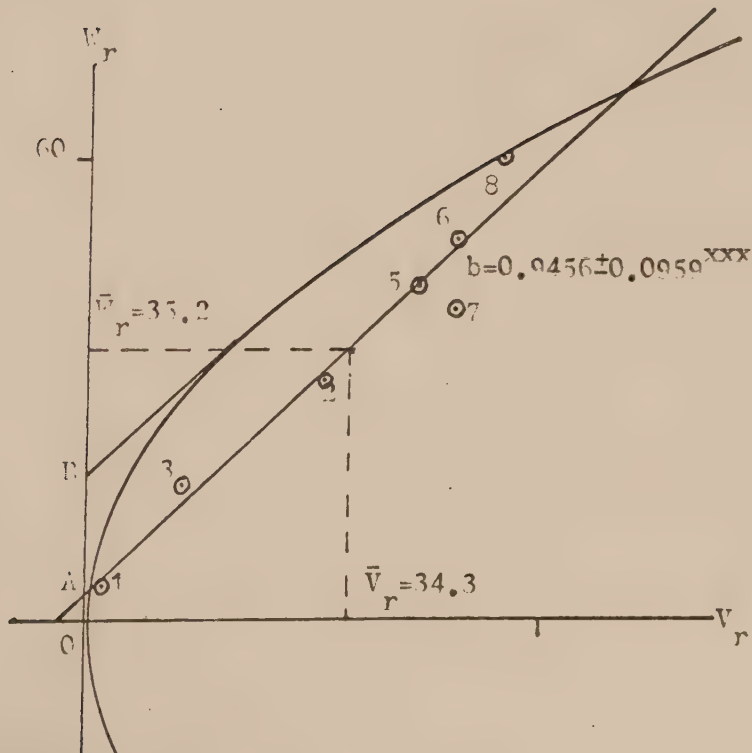


Fig. 6f. F_1 . Diallel VI-P₄. V_r, W_r graph.

x Significant at 5% level
 xx Significant at 1% level
 xxx Significant at 0.1% level

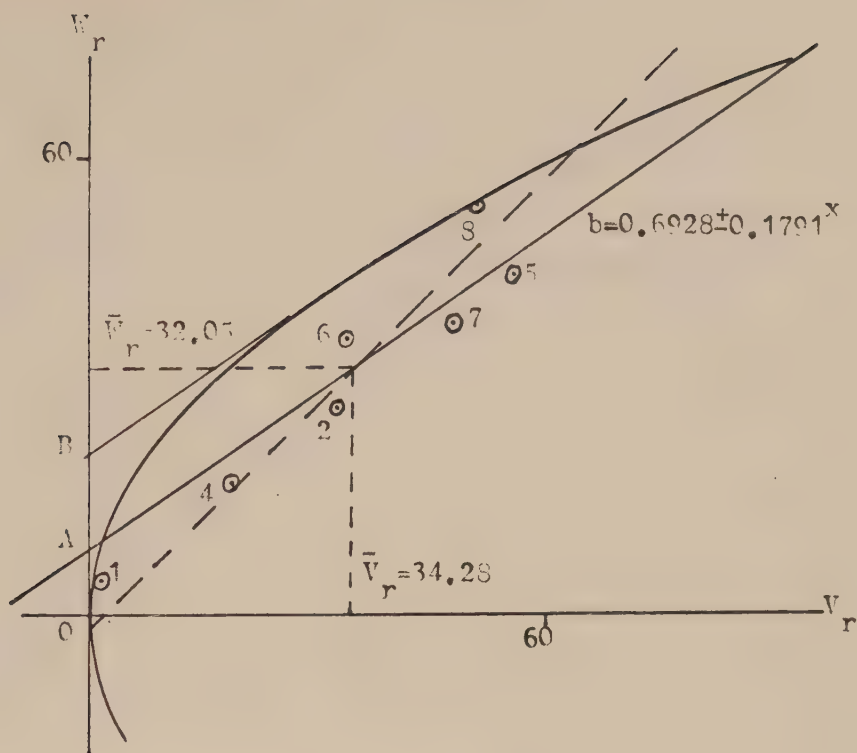


Fig. 6g. F_1 . Diallel VI- P_3 . V_r, W_r graph.

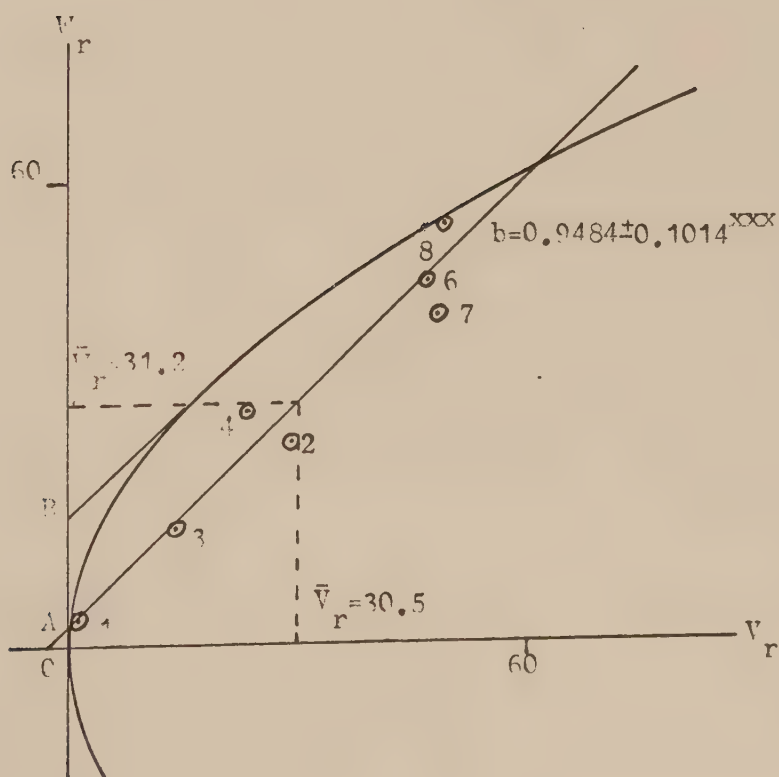


Fig. 6h. F_1 . Diallel VI- P_5 . V_r, W_r graph.

- x Significant at 5% level
- xx Significant at 1% level
- xxx Significant at 0.1% level

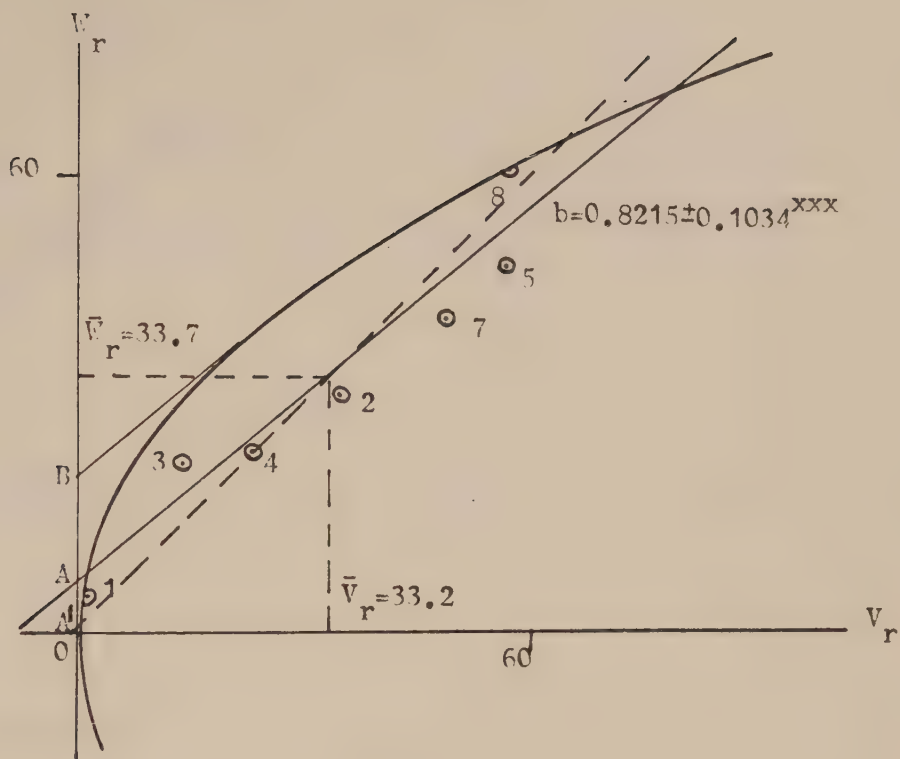


Fig. 6i. F₁. Diallel VI-P₆. V_r, W_r graph.

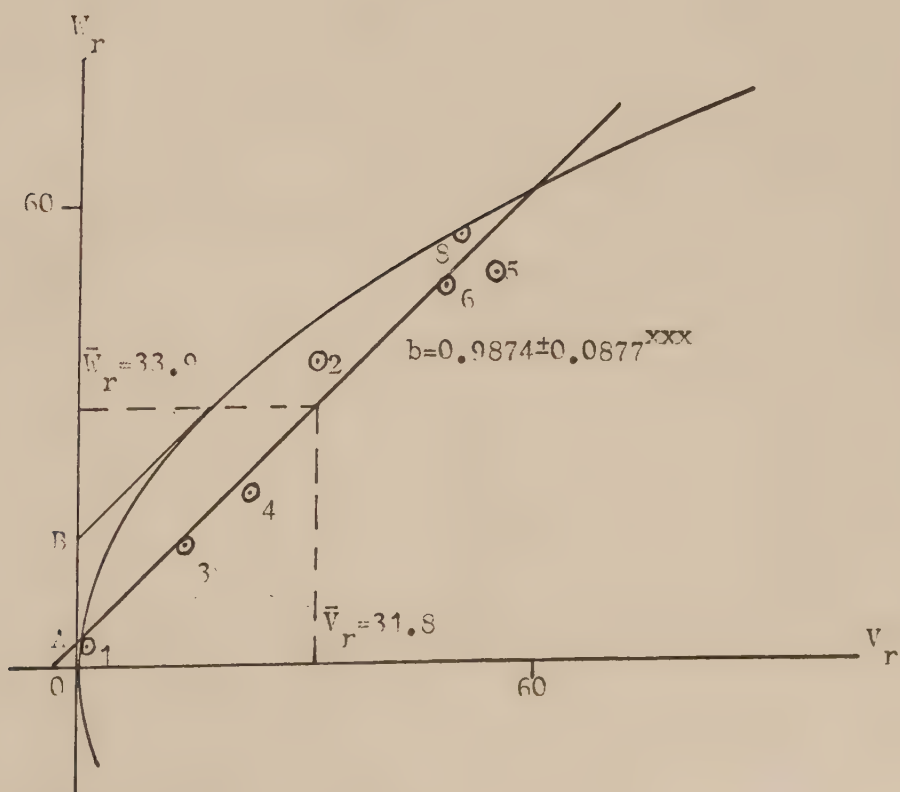
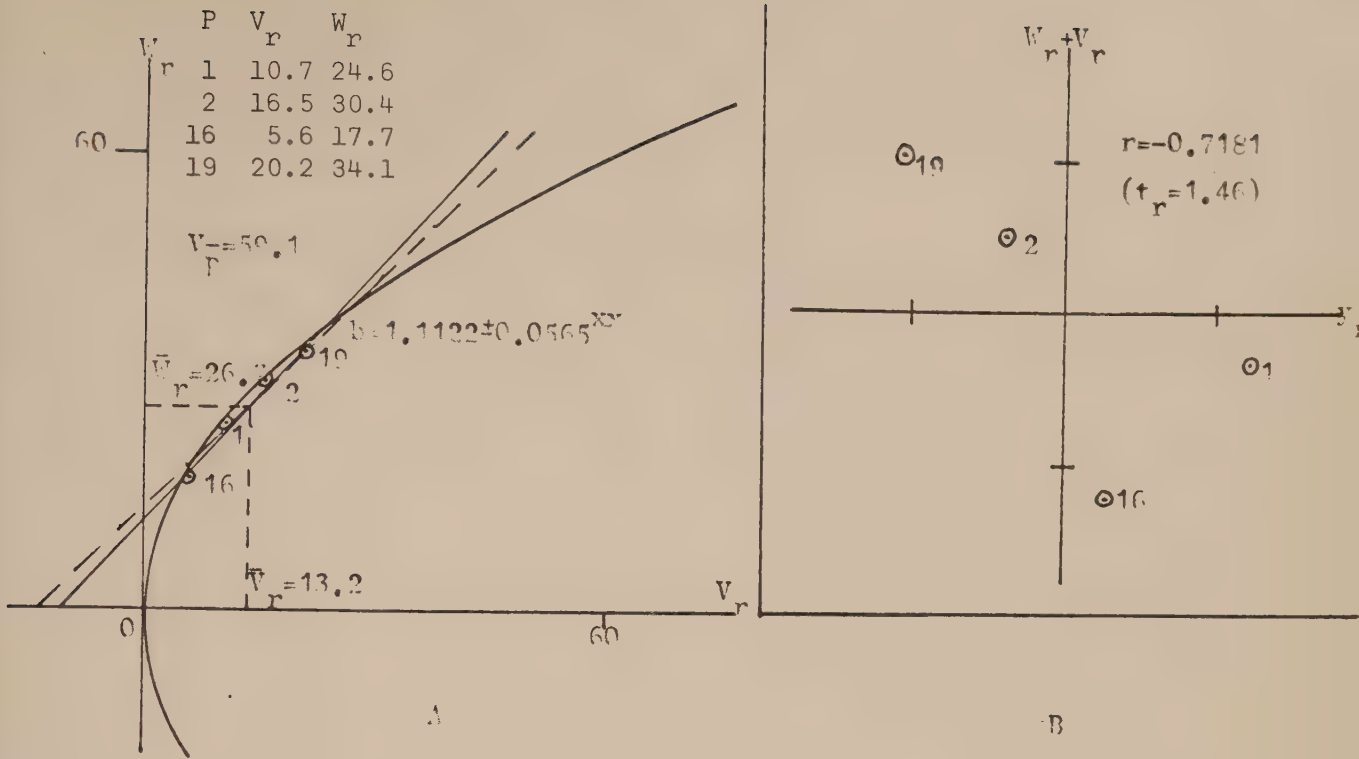
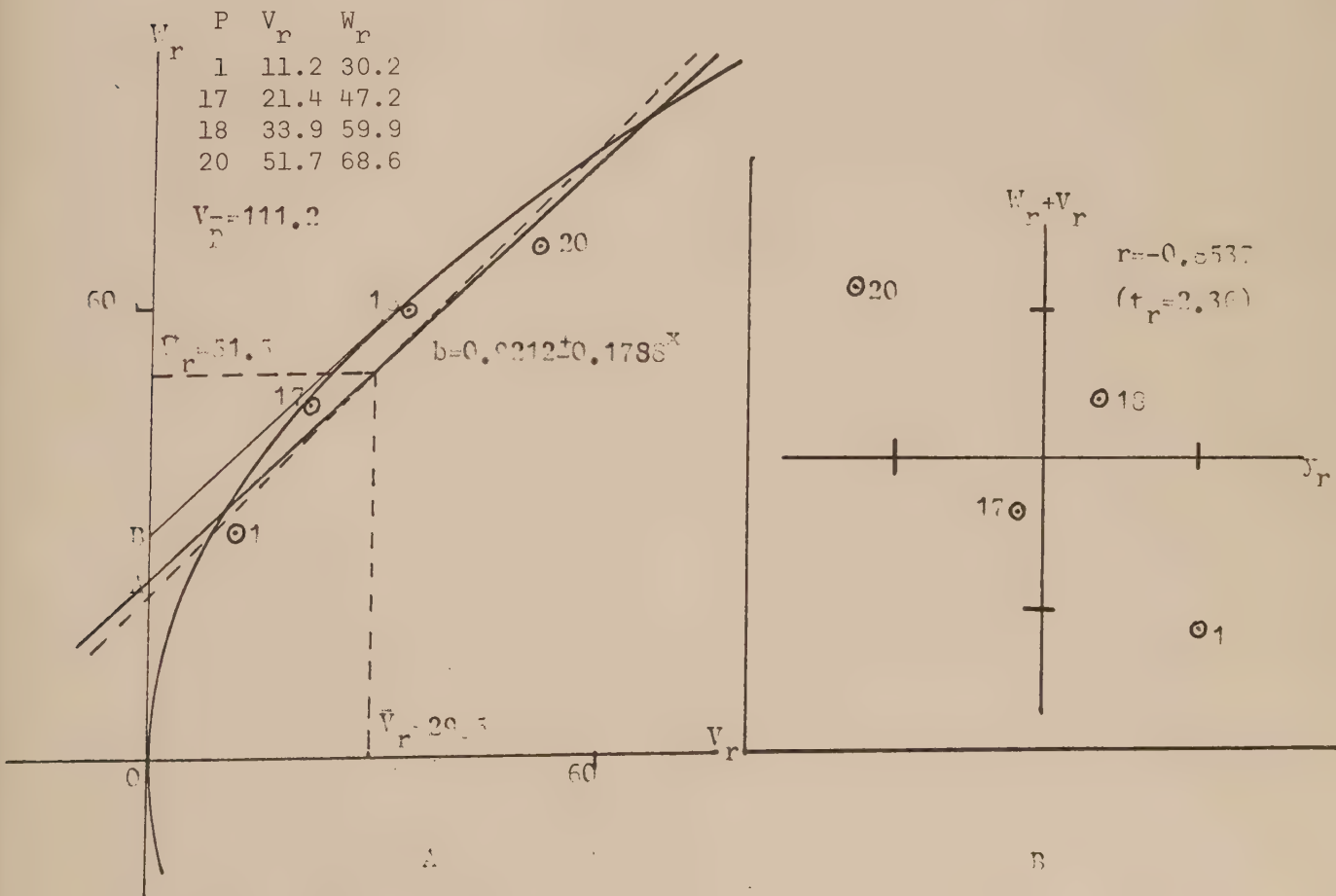


Fig. 6j. F₁. Diallel VI-P₇. V_r, W_r graph.

x Significant at 5% level
 xx Significant at 1% level
 xxx Significant at 0.1% level

Fig. 7. F_2 . Diallel VII.A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.Fig. 8. F_2 . Diallel VIII.A. V_r, W_r graph. B. Standardized deviation, y_r and $W_r + V_r$ graph.

x Significant at 5% level
 xx Significant at 1% level

Table 1. Name and numerical designations of Barley varieties (or ert-mutants) used as parents in diallel crosses.

Variety	No.	Used in diallel no.
Bonus	1	all
ert-a ²³	2	I, III, VI, VIa, VIb, VII
ert-c ⁵⁹	3	VI, VIa, VIb
ert-g ⁸⁰	4	VI, VIa, VIb
ert-a ²³ c ⁵⁹	5	VI, VIa, VIb
ert-a ²³ g ⁸⁰	6	VI, VIa, VIb
ert-c ⁵⁹ g ⁸⁰	7	VI, VIa, VIb
ert-a ²³ c ⁵⁹ g ⁸⁰	8	VI, VIa, VIb
ert-a ³⁶	9	II, IV
ert-c ³⁹	10	I, II
ert-c ⁹⁷	11	III, IV
ert-a ²³ c ³⁹	12	I, II, III, IV
ert-b ²	13	V
ert-i ²⁷	14	V
ert-b ² i ²⁷	15	V
ert-m ⁴⁰	16	VII
ert-a ¹³	17	VIII
ert-d ¹⁵	18	VIII
ert-a ²³ m ⁴⁰	19	VII
ert-a ¹³ d ¹⁵	20	VIII

Table 2. Spike density measurements in millimeter of Bonus and its ert-mutant varieties in a stand, 5 x 15 cm (Persson and Hagberg 1969)

Variety	Spike density (mm)
Bonus	29.8 $\pm$ 0.17
ert-a ¹³	19.6 $\pm$ 0.26
ert-a ²³	19.6 $\pm$ 0.10
ert-a ³⁶	19.4 $\pm$ 0.21
ert-b ²	21.5 $\pm$ 0.34
ert-c ³⁹	22.8 $\pm$ 0.27
ert-c ⁵⁹	23.5 $\pm$ 0.33
ert-c ⁹⁷	16.6 $\pm$ 0.34
ert-d ¹⁵	15.2 $\pm$ 0.23
ert-g ⁸⁰	23.2 $\pm$ 0.20
ert-i ²⁷	22.7 $\pm$ 0.22
ert-m ⁴⁰	24.8 $\pm$ 0.37

Table 3 a-b. Mean "ear length" values (mm) for half-diallel cross with Bonus and ert-mutant barley varieties. Parental values underlined.

Replication 1 (Diallel VIA)									Replication 2 (Diallel VIB)								
↵ Parent									↵ Parent								
1	2	3	4	5	6	7	8		1	2	3	4	5	6	7	8	
<u>1 33.0</u>	30.3	30.8	32.8	31.3	34.0	31.0	31.6		<u>1 33.9</u>	31.0	32.3	31.2	31.0	34.1	30.0	31.6	
2	<u>21.1</u>	29.7	30.7	18.8	21.9	31.0	18.5			<u>21.0</u>	30.4	30.8	19.2	21.8	30.1	19.2	
3		<u>27.5</u>	33.6	24.5	33.7	25.6	24.1	3			<u>27.7</u>	33.2	24.8	31.9	24.1	24.5	
4			<u>23.4</u>	30.8	24.7	25.6	22.2	4				<u>22.5</u>	30.1	22.8	22.6	22.0	
5				<u>13.4</u>	23.3	24.4	12.6	5					<u>13.3</u>	21.7	25.1	13.0	
6					<u>15.5</u>	24.9	17.3	6						<u>17.2</u>	24.6	17.4	
7						<u>15.2</u>	13.2	7							<u>13.7</u>	13.5	
8							<u>10.3</u>	8								<u>11.2</u>	

Table 4a. Mean values in mm of parents (underlined) and F₁-hybrids in five 4 x 4 diallel crosses (averaged over two replications in each case).

Diallel no.	Parent no.	Male array	Female array			
			Bonus	ert-a ²³	ert-c ³⁹	ert-a ²³ c ³⁹
I	1	Bonus	<u>32.50</u>	31.70	31.60	29.40
	2	ert-a ²³	31.05	<u>19.65</u>	31.00	18.70
	10	ert-c ³⁹	31.75	31.20	<u>26.70</u>	23.30
	12	ert-a ²³ c ³⁹	30.30	18.55	23.45	<u>12.60</u>
II			Bonus	ert-a ³⁶	ert-c ³⁹	ert-a ²³ c ³⁹
	1	Bonus	<u>32.35</u>	30.20	32.10	29.70
	9	ert-a ³⁶	30.35	<u>18.55</u>	30.20	18.65
	10	ert-c ³⁹	31.70	30.35	<u>26.20</u>	22.90
	12	ert-a ²³ c ³⁹	30.45	19.25	22.15	<u>12.95</u>
III			Bonus	ert-a ²³	ert-c ⁹⁷	ert-a ²³ c ³⁹
	1	Bonus	<u>33.10</u>	32.05	31.00	31.15
	2	ert-a ²³	32.70	<u>19.95</u>	29.40	18.85
	11	ert-c ⁹⁷	30.55	28.55	<u>17.65</u>	28.10
	12	ert-a ²³ c ³⁹	29.95	19.00	28.35	<u>12.85</u>
IV			Bonus	ert-a ³⁶	ert-c ⁹⁷	ert-a ²³ c ³⁹
	1	Bonus	<u>31.30</u>	30.35	31.30	30.70
	9	ert-a ³⁶	29.80	<u>19.10</u>	28.05	18.75
	11	ert-c ⁹⁷	30.85	28.85	<u>17.70</u>	28.00
	12	ert-a ²³ c ³⁹	31.35	18.90	27.40	<u>12.90</u>
V			Bonus	ert-b ²	ert-i ²⁷	ert-b ² i ²⁷
	1	Bonus	<u>32.00</u>	31.40	31.65	30.90
	13	ert-b ²	29.90	<u>22.60</u>	29.45	22.00
	14	ert-i ²⁷	31.45	30.10	<u>23.75</u>	23.55
	15	ert-b ² i ²⁷	30.20	21.60	21.10	<u>13.75</u>

Table 4b. Mean values in mm of parents (underlined) and F₁-hybrids in two 4 x 4 half-diallel crosses involving linkage (averaged over two replications in each case).

Diallel no.	Parent no.	Male array	Female array			
			Bonus	ert-a ²³	ert-m ⁴⁰	ert-a ²³ _m ⁴⁰
VII	1	Bonus	<u>35.7</u>	30.2	31.1	27.9
	2	ert-a ²³		<u>23.3</u>	28.1	21.5
	16	ert-m ⁴⁰			<u>28.4</u>	25.3
	19	ert-a ²³ _m ⁴⁰				<u>17.6</u>
VIII			Bonus	ert-a ¹³	ert-d ¹⁵	ert-a ¹³ _d ¹⁵
	1	Bonus	<u>35.7</u>	30.1	29.6	28.0
	17	ert-a ¹³		<u>22.4</u>	24.6	19.1
	18	ert-d ¹⁵			<u>28.2</u>	16.6
	20	ert-a ¹³ _d ¹⁵				<u>10.7</u>

Table 5. Analyses of variance of (Wr-Vr) values ("ear length")
in five sets of diallels, I-V.

Sources of variation	D.F.	Mean squares				
		Diallel I	Diallel II	Diallel III	Diallel IV	Diallel V
Arrays (lines)	3	0.7	1.5	190.2 [*]	175.3 ^{**}	5.8
Blocks (replications)	1	59.4	1.0	1.7	25.9	1.4
Error	3	4.7	1.1	15.5	5.9	2.0

* Statistically significant at the 5% level

** Statistically significant at the 1% level

Table 6. Analyses of variance for diallels I-V

Sources of variation	D.F.	Diallel I		Diallel II		Diallel III		Diallel IV		Diallel V	
		MS	P	MS	P	MS	P	MS	P	MS	P
a	3	305.1	<0.001	295.5	<0.001	234.9	<0.001	206.9	<0.001	221.1	<0.001
b ₁	1	138.5	<0.001	139.4	<0.001	330.0	<0.001	347.2	<0.001	135.3	<0.001
b ₂	3	1.0	0.05-0.01	1.4	0.05-0.01	21.9	<0.001	23.9	<0.001	0.4	-
b ₃	2	57.2	<0.001	50.4	<0.001	72.1	<0.001	52.2	<0.001	34.3	<0.001
b	6	42.7	<0.001	40.7	<0.001	90.0	<0.001	87.2	<0.001	34.2	<0.001
c	3	0.08	-	0.10	-	0.48	>0.20	0.27	-	2.48	0.05-0.01
d	3	0.38	>0.20	0.47	>0.20	0.47	>0.20	0.38	>0.20	0.63	>0.20
t	15										
B	1	0.34	-	0.41	-	0.50	-	2.10	-	0.70	-
Ba	3	0.05		0.07		0.33		0.73		0.43	
Bb ₁	1	0.65		0.00		0.10		0.10		0.10	
Bb ₂	3	0.28		0.10		0.20		0.07		0.13	
Bb ₃	2	0.57		0.41		0.75		0.25		0.35	
Bc	3	0.31		0.22		1.00		0.20		0.73	
Bd	3	0.04		0.96		0.07		0.53		1.23	
Bt	15	0.26		0.32		0.43		0.35		0.56	
Total	31										

Table 7. Estimates of parameters D , H_1 , H_2 , F , h^2 ; mean values; and related statistics from analyses of 5 separate diallel crosses for "ear length" in Bonus barley and its ert-varieties.

Statistics	D i a l l e l s				
	I	II	III	IV	V
V_{OLO}	74.41	72.84	75.03	61.31	55.76
W_{OLOI}	38.02	36.77	31.13	26.68	25.34
V_{ILI}	30.23	29.02	36.73	34.47	20.23
V_{OLI}	18.62	18.14	15.25	13.30	16.32
$\bar{P}$	22.86	22.51	20.94	20.25	23.02
$\bar{F}_1$	27.66	27.33	28.35	27.84	27.73
$D \pm SE$	74.41 $\pm$ 0.50	72.82 $\pm$ 0.78	75.03 $\pm$ 7.64	61.34 $\pm$ 7.29	55.72 $\pm$ 1.29
$H_1 \pm SE$	43.28 $\pm$ 1.45	42.07 $\pm$ 2.28	97.42 $\pm$ 22.32	92.53 $\pm$ 21.28	35.31 $\pm$ 3.75
$H_2 \pm SE$	46.44 $\pm$ 1.34	43.63 $\pm$ 2.10	86.07 $\pm$ 20.68	84.45 $\pm$ 19.72	15.62 $\pm$ 3.49
$F \pm SE$	-3.25 $\pm$ 1.28	-12.01 $\pm$ 2.01	25.62 $\pm$ 19.77	16.21 $\pm$ 18.85	10.23 $\pm$ 3.32
$h^2 \pm SE$	92.15 $\pm$ 0.91	92.14 $\pm$ 1.42	219.06 $\pm$ 13.98	231.01 $\pm$ 13.33	88.03 $\pm$ 2.36
$(H_1/D)^{\frac{1}{2}}$	0.76	0.75	1.13	1.22	0.79
$H_2/4H_1 (= \bar{u}\bar{v})$	0.26	0.25	0.22	0.22	0.11
$K (= h^2/H_2)$	1.98	2.10	2.52	2.73	5.62
$K_d/K_r = \frac{[(4DH_1)^{\frac{1}{2}} + F]}{[(4DH_1)^{\frac{1}{2}} + \bar{F}]}$	0.95	0.80	1.35	1.24	1.25
$(AB/OB)^{\frac{1}{2}}$	0.76	0.73	0.89	0.97	0.80
$(D-H_1) \pm SE$	31.13 $\pm$ 1.31	30.75 $\pm$ 2.05	-22.39 $\pm$ 20.11	-31.19 $\pm$ 19.21	20.41 $\pm$ 3.38
$b_{W_r V_r} \pm SE$	0.995 $\pm$ 0.053	0.976 $\pm$ 0.022	0.712 $\pm$ 0.153	0.745 $\pm$ 0.151	1.019 $\pm$ 0.061
V_{ILI}/W_{OLOI}	0.79	0.78	1.18	1.29	0.79
Order of dominance of parents, most dominant to most recessive genes.	1(10)2(12)	1(10)9(12)	1(11)2(12)	1(11)9(12)	1(14)(13)(15)
Correlation of $(W_r + V_r)$ and y_r	-0.9805	-0.9862	-0.8961 (t=2.85)	-0.9388 (t=3.97)	-0.9978

* Statistically significant at the 5% level

** Statistically significant at the 1% level

*** Statistically significant at the 0.1% level

Table 7 a. Values of V_r , W_r , V_p and (W_r+V_r) for diallels I-V.

P	Diallel I			P	Diallel II			P	Diallel III			P	Diallel IV			P	Diallel V		
	V_r	W_r	W_r+V_r		V_r	W_r	W_r+V_r		V_r	W_r	W_r+V_r		V_r	W_r	W_r+V_r		V_r	W_r	W_r+V_r
1	1.77	10.31	12.08	1	1.78	10.98	12.76	1	0.94	7.81	8.75	1	0.22	1.83	2.05	1	0.21	3.40	3.61
2	46.95	54.39	101.34	9	45.44	52.69	98.13	9	47.25	44.65	91.90	9	33.86	32.66	66.52	13	18.22	25.35	43.57
10	15.95	23.03	38.98	10	16.09	23.07	39.16	11	33.72	21.11	54.83	11	34.68	18.92	53.60	14	17.23	22.75	39.98
12	56.28	64.37	120.65	12	52.78	60.37	113.15	12	65.03	50.96	115.99	12	69.12	53.33	122.45	15	45.27	49.88	95.15
V_p	74.41				72.84				75.03				61.31				55.76		

Table 8 a. Analysis of variance of 8 x 8 half-diallel tables.

Diallel No.	Sources	D.F.	Sum of squares	M.S.	P
VI (using means over two replications)	a	7	1111.9	158.8	< 0.001
	b ₁	1	225.6	225.6	< 0.001
	b ₂	7	25.0	3.5	< 0.001
	b ₃	20	144.9	7.2	< 0.001
	Total	35	1507.4		
	Error	35		0.26	
VI a (Rep. 1)	a	7	1126.1	160.8	< 0.001
	b ₁	1	243.0	243.0	< 0.001
	b ₂	7	30.7	4.4	< 0.001
	b ₃	20	275.6	13.8	< 0.001
	Total	35	1675.4		
	Error			0.26	
VI b (Rep. 2)	a	7	1105.4	157.9	< 0.001
	b ₁	1	208.9	208.9	< 0.001
	b ₂	7	19.3	2.7	< 0.001
	b ₃	20	275.6	13.8	< 0.001
	Total	35	1609.2		
	Error			0.26	

Table 8 b. Analysis of variance of F_1 trial for diallel VI.

Sources	D.F.	M.S.	VR	Error for the diallel
Populations	35	93.2	***	
Replications	1	0.85	—	
Error	35	0.52	—	0.26

*** Statistically significant at the 0.1% level

Table 8 c. Values of V_r , W_r , V_p^- and $(W_r + V_r)$ for diallels VI, VIA and VIB.

Parent	Diallel VI (over 2 reps.)			Diallel VIA (Rep.No. 1)			Diallel VIB (Rep.No. 2)		
	V_r	W_r	$W_r + V_r$	V_r	W_r	$W_r + V_r$	V_r	W_r	$W_r + V_r$
1	1.61	3.55	5.16	1.6	1.3	2.9	2.9	6.2	9.1
2	31.38	29.24	60.62	31.9	29.7	61.6	30.9	28.9	59.8
3	14.37	17.04	31.41	14.9	14.4	29.3	14.5	19.8	34.3
4	21.39	22.60	43.99	20.1	22.3	42.4	23.2	23.1	46.3
5	48.22	41.50	89.72	49.9	42.4	92.3	46.8	40.4	87.2
6	41.20	42.04	83.24	45.1	43.8	88.9	38.0	40.7	78.7
7	41.26	34.97	76.23	42.6	36.6	79.2	40.6	33.7	74.3
8	48.21	53.38	101.59	49.7	53.5	103.2	46.8	53.3	100.1
V_p^-	60.33			59.8			61.4		

Table 9. Regression coefficients; order of dominance; probability values for heterogeneity of ($W_r - V_r$) test, and significant differences of regression from unity for the eight 7 x 7 half-dials.

Excluded parent	t^2 -test for heterogeneity of ($W_r - V_r$)	Test for significant difference (t_D) of the regression line from unit slope	$b_{W_r V_r} \pm \text{SE}$	Order of dominance of the parents determined by ($W_r + V_r$)
P ₁	P > 0.2	P ≈ 0.05 ($t_D = 2.585$)	0.4133 ± 0.2267 ($t = 1.82$)	3426875
P ₂	P > 0.9	P > 0.5	0.9570 ± 0.0714 ^{xxxx}	1347658
P ₃	P > 0.6	P > 0.1	0.6928 ± 0.1791 ^x	1426758
P ₄	P > 0.9	P > 0.5	0.9456 ± 0.0959 ^{xxxx}	1325768
P ₅	P > 0.9	P > 0.6	0.9484 ± 0.1014 ^{xxxx}	1342768
P ₆	P > 0.9	P > 0.1	0.8215 ± 0.1034 ^{xxxx}	1342758
P ₇	P > 0.9	P > 0.8	0.9874 ± 0.0877 ^{xxxx}	1342658
P ₈	P > 0.7	P > 0.05	0.8361 ± 0.0608 ^{xxxx}	1342756

x Statistically significant at the 5% level
xxx Statistically significant at the 0.1% level

Table 9 a. Analysis of variance of 7 x 7 half-diallel tables. (Extracted from 8 x 8 diallel VI, excluding parents one at a time.)

Sources	D.F.	Mean squares							
		Excl. P ₁	Excl. P ₂	Excl. P ₃	Excl. P ₄	Excl. P ₅	Excl. P ₆	Excl. P ₇	Excl. P ₈
a	6	112.5	167.2	156.2	167.1	142.8	155.9	161.2	84.3
b ₁	1	192.8	200.4	200.6	173.4	180.4	172.4	168.1	234.2
b ₂	6	6.3	3.8	4.7	5.3	1.5	4.1	3.0	3.7
b ₃	14	13.8	14.1	15.1	14.6	14.5	15.9	13.4	14.4
Total	27								
Error	27	0.26	0.30	0.25	0.20	0.30	0.23	0.20	0.30

All Mean square values (unless marked) are statistically significant at 0.1% level.
 ** Statistically significant at 1.0% level.

Table 9 b. Analysis of variance of F₁ trials for 7 x 7 diallels (Extracted by excluding parents one at a time from 8 x 8 diallel VI.)

Sources	D.F.	Mean squares							
		Excl. P ₁	Excl. P ₂	Excl. P ₃	Excl. P ₄	Excl. P ₅	Excl. P ₆	Excl. P ₇	Excl. P ₈
Popula- tions	27	80.6	104.2.	101.4	103.9	91.6	99.3	98.2	70.3
Replica- tions	1	1.1	1.5	0.9	0.01	0.8	0.3	0.01	1.9
Error	27	0.53	0.61	0.51	0.40	0.60	0.47	0.41	0.61
Error for the diallel		0.26	0.30	0.25	0.20	0.30	0.23	0.20	0.30

*** Statistically significant at 0.1% level.

Table 9 c. Estimates of parameters D, H₁, H₂, F, h², mean values and related statistics from analyses of 7 x 7 half-diallels (seven diallels from 8 x 8 half diallel No. VI by excluding one parent at a time).

Statistics	Excl. P ₁	Excl. P ₂	Excl. P ₃	Excl. P ₄	Excl. P ₅	Excl. P ₆	Excl. P ₇	Excl. P ₈
V _{OL0}	35.9	70.1	59.3	68.7	60.0	67.8	64.5	54.1
W _{OL0I}	21.3	35.8	32.0	35.2	31.2	33.7	33.9	21.4
V _{ILI}	28.9	34.1	34.2	34.3	30.5	33.2	31.8	24.1
V _{OLI}	13.8	18.8	18.3	19.2	16.2	17.4	18.6	8.3
D	35.9	70.1	59.3	68.7	60.0	67.8	64.5	54.1
F	-13.4	-3.0	-9.4	-3.4	-4.8	0.8	-6.6	22.6
H ₁	66.3	63.3	68.1	65.1	57.2	65.8	56.1	64.9
H ₂	60.4	61.2	63.6	60.4	57.2	63.2	52.8	63.2
h ₂	148.8	231.0	148.8	129.9	134.5	129.9	125.4	179.5
P	18.0	19.8	18.9	19.5	20.9	20.5	20.8	21.3
F ₁	24.1	26.0	25.0	25.2	26.7	26.2	26.4	28.0
H ₂ /4H ₁	0.22	0.24	0.23	0.23	0.25	0.24	0.23	0.24
Kd/Kr	0.75	0.94	0.86	0.95	0.92	1.01	0.89	1.47
K(h ² /H ₂)	2.4	2.5	2.3	2.1	2.3	2.0	2.3	2.8
(H ₁ /D) ¹ / ₂	1.34	0.94	1.07	0.96	0.97	0.98	0.92	1.09
(AB/OB) ¹ / ₂	0.74	0.91	0.74	0.90	0.93	0.82	0.90	0.95
(A ¹ B/OB) ¹ / ₂	1.14	-	1.04	-	-	0.97	-	1.07

Table 9 d. Values of V_r , W_r and V_p^- for 7 x 7 diallels.

Parent	Excl. P_1		Excl. P_2		Excl. P_3		Excl. P_4		Excl. P_5		Excl. P_6		Excl. P_7		Excl. P_8	
	V_r	W_r	V_r	W_r	V_r	W_r	V_r	W_r	V_r	W_r	V_r	W_r	V_r	W_r	V_r	W_r
1	-	-	1.6	4.4	1.8	4.6	2.4	4.2	1.7	3.2	0.9	5.6	1.5	2.7	1.9	3.7
2	31.2	20.5	-	-	32.4	27.3	31.0	31.0	29.4	26.2	34.3	31.7	31.4	39.6	28.6	22.7
3	15.2	12.4	16.9	19.7	-	-	12.4	17.2	14.2	15.0	13.5	22.7	14.0	15.8	12.1	12.2
4	21.0	14.7	23.3	25.9	18.2	17.7	-	-	23.7	30.3	22.8	24.0	22.8	22.8	19.5	17.0
5	41.4	25.8	54.5	49.2	55.2	45.1	43.7	43.8	-	-	56.6	48.7	55.1	51.0	38.9	34.0
6	29.5	23.7	47.4	49.6	33.9	36.5	48.4	49.4	47.5	46.9	-	-	48.0	49.6	39.2	37.0
7	38.6	22.6	38.8	39.5	47.7	38.7	48.0	40.4	48.2	42.6	48.2	41.9	-	-	28.8	23.1
8	25.5	29.7	56.5	62.4	50.6	54.4	54.3	60.4	49.2	54.5	56.1	61.4	50.4	56.4	-	-
V_p^-	35.9		70.1		59.3		68.7		62.0		67.8		64.5		54.1	

Table 10 a. Analysis of variance of 4 x 4 half-diallel tables (F_2 involving linkage).

Diallel No.	Sources	D.F.	Sum of squares	M.S.	P
VII (over two replications)	a	3	233.0	77.7	<0.001
	b ₁	1	2.9	2.9	0.05-0.01
	b ₂	3	2.5	0.8	0.20-0.10
	b ₃	2	3.4	1.7	0.10-0.05
	Total	9	241.8		
	Error	9		0.43	
VIII (over two replications)	a	3	462.6	154.2	<0.001
	b ₁	1	0.4	0.4	-
	b ₂	3	23.1	7.7	<0.001
	b ₃	2	8.9	4.4	0.01-0.001
	Total	9	495.0		
	Error	9		0.33	

Table 10 b. Analysis of variance of F_2 trials for diallel VII and VIII.

Sources	D.F.	M.S.	V.R.	Error for the diallel
<u>Diallel VII</u>				
Populations	9	53.02	***	
Replications	1	0		
Error	9	0.86		0.43
<u>Diallel VIII</u>				
Populations	9	110.06	***	
Replications	1	0.01		
Error	9	0.65		0.33

*** Statistically significant at the 0.1% level.

Table 10 c. The analysis of the variance of Wr-Vr for the
4 x 4 half-diallels VII and VIII.

Sources	D.F.	Diallel VII		Diallel VIII	
		Mean square	P	Mean square	P
Lines	3	1.54	>0.05	38.37	>0.05
Blocks	1	45.60		2.21	
Error	3	0.34		4.63	

Table 11. Estimates of parameters D , H_1 , H_2 , F , h^2 , mean values, and related statistics from analyses of 3 separate diallel crosses for "ear length" in Bonus barley and its ert-varieties.

Statistics	Diallels		
	VI	VII	VIII
V_{OLO}	60.3	59.1	111.2
W_{OLOI}	30.5	26.7	51.5
V_{ILI}	30.9	13.2	29.5
V_{OLI}	16.2	12.3	24.9
$\bar{P}$	19.9	26.2	24.2
$\bar{F}_1$	26.0	27.6	27.2
$D \pm S.E.$	60.3 $\pm$ 1.74	59.1 $\pm$ 0.22	111.2 $\pm$ 3.69
$H_1 \pm S.E.$	62.0 $\pm$ 4.02	5.1 $\pm$ 0.64	23.2 $\pm$ 10.72
$H_2 \pm S.E.$	58.9 $\pm$ 3.49	3.6 $\pm$ 0.60	18.4 $\pm$ 9.90
$F \pm S.E.$	-1.5 $\pm$ 4.13	11.4 $\pm$ 0.57	16.4 $\pm$ 9.48
$h^2 \pm S.E.$	145.0 $\pm$ 2.34	7.5 $\pm$ 0.40	35.0 $\pm$ 6.71
$(H_1/D)^{\frac{1}{2}}$	1.00	0.28	0.44
$H_2/4H_1 (= \bar{u}\bar{v})$	0.23	0.17	0.19
$K (=h^2/H_2)$	2.46	2.07	1.90
K_d/K_r	0.97	1.98	1.38
$(AB/OB)^{\frac{1}{2}}$	0.90	0.33	0.43
$(D-H_1) \pm S.E.$	-1.6 $\pm$ 3.45	54.0 $\pm$ 0.59	88.0 $\pm$ 9.66
$b_{W_r V_r} \pm S.E.$	0.9033 $\pm$ 0.0938	1.1122 $\pm$ 0.0565	0.9212 $\pm$ 0.1788
V_{ILI}/W_{OLOI}	1.01	0.49	0.57
Order of dominance of parents. Most dominant to most recessive genes.	13427658	(16)(1)(2)(19)	(1)(17)(18)(20)
Correlation of $(W_r + V_r)$ and y_r	-0.9977 ^{xxx}	-0.7181 ($t_r=1.45$)	-0.8537 ($t_r=2.30$)

xxx Significant at the 0.1% level

Table 12. Values of V_r , W_r , V_p and (W_r+V_r) for diallels VII and VIII.

Parent	Diallel VII			Parent	Diallel VIII		
	V_r	W_r	W_r+V_r		V_r	W_r	W_r+V_r
1	10.7	24.6	35.3	1	11.2	30.2	41.4
2	16.5	30.4	46.9	17	21.4	47.2	68.6
16	5.6	17.7	23.3	18	33.9	59.9	93.8
19	20.2	34.1	54.3	20	51.7	68.6	120.3
V_p	59.1				111.2		

